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MODELS AND METHODOLOGIES IN EVOLUTIONARY THEORY

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PREFACE

During the academic years 1976–1977, the University of Pittsburgh and the Carnegie Museum of Natural History jointly sponsored two colloquia series dealing with aspects of evolution, "Models and Methodologies in Evolutionary Theory."

The first year's participants were:

Niles Eldredge, The American Museum of Natural History;
Steven Jay Gould, The Museum of Comparative Zoology, Harvard University;
David M. Raup, University of Rochester;
Thomas J. M. Schopf, University of Chicago;
Eugene S. Gaffney, The American Museum of Natural History.

Those of the second series were:

Albert A. Bartlett, University of Colorado;
Robert J. Baker, Texas Tech University;
Walter J. Bock, Columbia University;
Steven M. Stanley, Johns-Hopkins University;
Leonard Radinsky, University of Chicago.

Each participant presented two formal talks and five also submitted original manuscripts for publication. The latter include three papers on approaches to evolutionary theory (Eldredge, Bock, and Baker); one discussing the evolutionary consequences of preservational biases of the fossil record (Raup); and another dealing with philosophy and methodology in phylogeny reconstruction, in this case the origin of Tetrapoda (Gaffney).

We are indebted to Dr. Craig C. Black, Director, Carnegie Museum of Natural History, and the Provost's Office, University of Pittsburgh, for generously funding these colloquia and providing the necessary facilities and equipment. Among the many of both institutions who helped to make these colloquia successful, we wish to especially thank Dr. R. Raikow and Mr. J. Harper (University of Pittsburgh) and Drs. M. Dawson, H. Genoways and L. Krishtalka (Carnegie Museum of Natural History). In addition, we wish to acknowledge the editorial assistance of Ms. G. LoAlbo.

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ALTERNATIVE APPROACHES TO EVOLUTIONARY THEORY

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INTRODUCTION

To most North Americans who have ever thought about evolution at all, there is only one "evolutionary theory"—"neo-darwinism." We look askance upon other sets of explanations of evolution, such as the various versions of saltationism, much in the way that Judaeo-Christian tradition views devotion to any but the One God. My purpose here is not to espouse pagan alternatives to orthodox darwinism, but rather to develop the theme that neo-darwinian theory is not at all as monolithic as we might suppose. Rather, *all* evolutionary thinking, darwinian and non-darwinian, pre- and post-1859, has been beset by a curious duality, which has effectively hindered a truly integrated theory of any guise from emerging.

Evolution can be viewed in two basic ways. If evolution is "descent with modification" (Darwin, 1859:171) or "change in the genotype of a population" (Dobzhansky, 1951:21), then we must ask how that change occurs. What are the mechanisms? Whether we are discussing genes, their phenotypic expression, physiology, or behavior, variation and factors of heritability lie at the core of the problem. Thus, any standard text properly devotes much of its space to genetics, and mutation, recombination, natural selection and related concepts weigh heavily in our theories of evolutionary mechanics.

Darwin (1859) also gave us our other basic way of looking at evolution—the "origin of species." We see around us today perhaps as many as two million discrete species. If we assume, as seems reasonable, that species are real entities in nature, their origins must be explained, and because species are aggregates of populations, which are themselves aggregates of individuals, the mechanics of speciation do not seem immediately reducible to the principles of genetics (see for example, Avise and Ayala, 1975). Thus, standard texts also devote a good deal of space to speciation.

No one would argue that we can have an evolutionary theory without either one of these two components. A theory is simply incomplete if it lacks either a set of statements concerning (1) changes in genes and their expression or (2) the origins of new species. The problem with neo-darwinian theory today is not that it lacks one or the other of these components, but that they have as yet to be successfully fully integrated.

This problem comes into focus more sharply if we first generalize these two aspects of the evolutionary process. The first aspect can be labelled the "transformational approach"; under this approach, the central question in evolution is: how do genes and their products become modified in the evolutionary process? How are karyotypes, behavior, pelage colors, hormones, and so on, modified by the evolutionary process?

In darwinian theory, natural selection is the key concept of the transformational approach, and evolutionary adaptation seems to be the prime focus of most of the research conducted from this point of view. Trends, adaptive radiations, rates of morphologic change, and even the origin of taxa of higher categorical rank (which superficially sounds as though it belongs under the "taxic approach") are examples of the kinds of evolutionary topics typically addressed by paleontologists and others. These problems are almost entirely defined in terms of the central issue of the transformational approach: how are these particular biochemical, cytological, anatomical, physiological, and behavioral traits changed in evolution? An adaptive radiation, for example, is viewed as a problem of divergent anatomical specializations among a series of related organisms, rather than as a spectrum of discrete species occupying a diverse array of ecological niches. The emphasis in this approach on morphologic (*sensu lato*) change inevitably results in the entire disregarding of taxa in the analysis. And thus we have, particularly in the literatures of genetics and paleontology, a large corpus of statements pertaining to the nature of the evolutionary process which almost completely ignores the existence of taxa and the problem of their origins.

Concern for species and other taxa under the transformational approach is limited to use of Linnaean names to refer to complexes of anatomical (or genetic, physiologic, and others) traits. Indeed, most adherents of this approach implicitly or explicitly deny the “reality” of species as discrete entities in nature. For if species are not considered as real, discrete entities, the problem of their origin may of course be safely ignored, and we need not be concerned with integrating speciation theory with the concerns of genetic and morphologic transformation. This attitude is especially prevalent in paleontology and takes several guises. The more obvious, transparent version of the “non-reality” of species is well developed in Shaw (1969) whose main point concerning species is that they are neither operationally nor objectively recognizable, hence can be considered in this sense not to exist. Having thus done away with species as something to be concerned with, Shaw is then at liberty to develop a strategy for analyzing phylogenetic lineages (for the express purpose of correlating rock sequences) which pays no attention to component taxa, but instead focuses on correlation of particular character states.

For a far more subtle rejection of species as objects of central interest in evolutionary theory, consider the work of Simpson (for example, 1944, 1951, 1953). Simpson (for example, 1951) does not reject outright the reality of species[1]. But he does deny their discreteness, as in his rejection of the “genetical definition” of species in favor of a concept of species in evolutionary time: “An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.” (Simpson, 1961:153, modified slightly from Simpson, 1951:289). Thus, though any lineage may, obviously, have a definite beginning and a definite end (that is, “extinct without issue” as opposed to “extinction by transformation”—see Simpson, 1974:14 for an example of the use of these concepts), the door is purposely left open for anything from negligible to vast amounts of morphological or genetical transformation within the indefinite time segment of this lineage. This is a rather elusive concept of the species, though it may be the best we can have. It is apparent that Simpson's sincere attempt to formulate a more “evolutionary” concept of “species” stemmed from the historical consensus—by no means restricted to paleontology—which views evolution solely as change through time of genes and their products. Such change is construed as an almost inevitable consequence of the mere passage of time. And, of course, this is a reflection of the transformational approach. Simpson's definition, however different in intent from Shaw's (1969) explicit rejection of species, has the identical effect of removing the necessity of considering the origin of species when we confront the tempos and modes of evolution. In one guise or another, the transformational approach to evolution ignores species and hence is under no obligation to integrate speciation theory into the paradigm. If species are not real, or are at best arbitrarily delineated segments of lineages, speciation can safely be viewed as a useful adjunct to evolutionary theory, which merely tells us how new lineages get going in the first place. But the nearly total neglect of speciation by paleontologists and others wedded to the transformational approach can only imply that the truly interesting and meaningful evolutionary phenomena take place subsequent to the origin of a lineage (*sensu* Simpson, as cited above).

The second, or “taxic” approach, looks at evolution the other way around. Under this view, the central issue is: how do new taxa (usually species) originate? A fundamental assumption under this approach, of course, is that, at some level, aggregates of individuals (populations, perhaps species) are actual and discrete entities in nature, with their own roles in the economy of nature.

Speciation is the basic evolutionary model under the taxic approach. There are many particular models of speciation in the neo-darwinian literature (see Bush, 1975, for a useful review, as well as a stimulating advocacy of sympatric speciation). If fault can be found with the taxic approach, it is simply that its adherents have tended to limit themselves to the topic of speciation. But those who work primarily under the taxic approach have, from time to time, addressed the same variety of topics studied under the transformational approach, and have shown, with varying degrees of success, how the same problems may be addressed through the taxic approach.

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[1] The argument about the “reality” of taxa of different categorical rank is an old and interesting one. As may be anticipated, all possible views have been taken from time to time. Thus Simpson (1953:350) has rejected the idea expressed by Willis (1940) and others who claim that kingdoms appear first, followed by phyla, classes, and so forth; in terms of actual evolutionary mechanics, to nearly everyone's evident satisfaction, the evolutionary process goes on at the within- and among-population level. We inductively assume this to have been the case since life began. In this sense, genera and taxa of even higher categorical rank simply do not exist in the same sense as do species and populations. Ghiselin (1974) has recently stated this most cogently, insisting that species are individuals, not classes, and have a specifiable economic role in nature not possessed by taxa of higher categorical rank (which he calls “classes”). Inasmuch as it is populations, rather than species, which are economically integrated into ecosystems, it is perhaps preferable to bestow the quality of “reality” on them rather than species; others would prefer individuals. In any case, a counterargument has recently appeared among the phylogenetic systematists (for example, Bonde, 1974:567). In this view, all monophyletic groups, of whatever rank, are equally real, presumably in the sense that they are all defined and recognized in the same fashion. Though there is an appealing quality to this argument, considerations of ecological integration cause me to favor the view that populations, and perhaps species, are endowed with an aspect of “reality” not shared by taxa of higher categorical rank.

The crucial point here is that, under the taxic approach, the key concepts of adaptation and selection, as well as the remainder of the principles of population genetics, have not been lost sight of in speciation theory. Rather, no matter how unsatisfyingly and incompletely, they have been integrated with speciation theory. Thus, all the mechanisms invoked under the transformational approach (except some of the fanciful, nonexistent ones, such as "orthogenesis") are very much a part of both the problems addressed and the mechanisms invoked under the taxic approach. The reverse is simply not true—for the transformational approach to operate, at least to date, a prime requisite has been either the outright denial of the existence ("reality") of species or denial of their discreteness, to the extent that the problem of their origin can safely be viewed as a special case, or at most as a small part of the general problem. Because both speciation theory and genetic mechanisms are required in a complete theory, we are justified in rejecting *a priori* any segment of evolutionary theory as at best incomplete, and at worst irrelevant, if it does not contain elements of both. The taxic approach, thus far, at least, offers the only promise of complete integration—under the taxic approach, we are free to investigate mode and degree of genetic and morphologic change in the context of speciation. Under the transformational approach we must ignore the origin of species and view them as *a posteriori* products of the mind of the systematist who uses the results of evolution (genetic and morphologic change) to recognize, name, and pigeon-hole taxa. It must still be shown, however, that the same questions raised under the transformational approach can effectively be attacked under the taxic approach.

It is possible to examine the various subdisciplines of evolutionary biology (genetics, ecology, systematics, and paleontology—this list is perhaps not all-inclusive; certainly there is a large amount of overlap among these four semiarbitrarily delineated fields) and assess the relative degrees to which each of the two approaches has contributed to past and present theoretical work. Certainly elements of both appear in each of these disciplines. For true integration we must take genetics and see how it looks in the context of speciation (see Ayala, 1975, for a valuable review), look at ecological controls of speciation and of the resultant patterns of species diversity, and then turn to systematics and paleontology to look at patterns of taxic evolution in time as well as in space. Only then shall we be effectively translating the genuine problems posed under the transformational approach into the realistic terms of the taxic approach. The remainder of this paper treats just one of the disciplines—paleontology—and restates in taxic terms a single example of an evolutionary problem traditionally formulated and addressed in terms of the transformational approach. But the basic view expressed can be applied to any branch of evolutionary biology and to any problem usually expressed in terms of the transformational approach.

PALEONTOLOGICAL APPROACH TO EVOLUTIONARY THEORY

By the very nature of its materials, paleontology can have nothing direct to say about evolutionary mechanisms. Using fossils, we cannot study mutation, recombination, and selection with any degree of practicality, and certainly these and related concepts would never have come from paleontology. Likewise our modern concepts of speciation, while perhaps less difficult to apply to paleontogical data, do not emerge as self-evident precepts when one examines data on the fossil record. Both these aspects of evolutionary theory are quite difficult to relate hypothetico-deductively to the fossil record. Thus, the relationship between paleontology and evolutionary theory has been mostly a matter of application of neontological concepts to paleontological data and it is indeed difficult to identify any coherent segment of evolutionary theory, no matter how broadly construed, as having originated in paleontology.

In an evolutionary context, paleontologists have always had the option of looking at the fossil record, in either or both of two ways—(1) distributions in space and time of discrete taxa, which differ among themselves to a greater or lesser extent, and (2) distributions in space and time of different states of morphological characters assumed to be evolving. The post-1859 history of paleontology reveals a nearly total dedication to the transformational approach as opposed to the taxic approach to evolutionary problems. Waagen's (1869:185 ff) study of the evolution of "*Ammonites subradiatus*," in which he coined the expression "mutation," is an early exception to this generalization. As pointed out by Simpson (1942:48; 1953:81) Waagen's "mutations" were actually discrete taxa, an early example of the taxic approach to evolutionary studies in paleontology. But the preponderance of subsequent studies in evolutionary theory fall clearly into the transformational camp—to cite but a few outstanding examples, consider Rowe (1899) on Cretaceous echinoids, Carruthers (1910) on Carboniferous corals, Trueman (1922) on Jurassic oysters, and Brinkmann (1929) on Jurassic ammonites. This work culminated in the general syntheses of Simpson (1944, 1953), who integrated paleontological data and concepts with many of the evolutionary concepts of the rest of the "modern synthesis"—with the notable exception of speciation theory.

We might well wonder why paleontology remained on the whole oblivious to the taxic view of the evolutionary process when other areas of biology—particularly ecology and systematics—early on become aware of the problem of diversity posed by the existence of discrete taxa. The works of Wagner (1869) and Romanes (for example, 1886) (cited by Mayr, 1963) were early forerunners of the works of Mayr (for example, 1942, 1963), which remain the most complete and thorough statements of the taxic view of the evolutionary process in the English language[2]. But only in relatively recent years has the basic thrust of paleontological evolutionary thought begun to switch over to the taxic approach. This change is symbolized by the titles and contents of the two most recent book-length treatments of evolution by paleontologists—Valentine's (1973) "Evolutionary Paleoecology of the Marine Biosphere" and Boucot's (1975) "Evolution and Extinction Rate Controls." To both of these authors, evolution consists essentially of the origin, maintenance, and degradation of diversity—a purely taxic approach to evolution. There is indeed little in common between these two books on the one hand, and those of Simpson (especially 1944 and 1953) on the other. Many of the issues Simpson raised and discussed so ably under the transformational approach are given short shrift by Boucot (1975) and Valentine (1973)—including origin of taxa of higher categorical rank, trends, adaptive radiations, morphologic evolutionary rates (usually considered "macroevolutionary" topics—Simpson's "major features") as well as microevolutionary problems centering around species. Inasmuch as evolution seems to be more than merely the origin, maintenance, and degradation of diversity, we should continue to look for a fuller integration of the issues that Simpson and other paleontologists have addressed under the transformational approach, with the basically taxic/ecological approach advocated by Valentine, Boucot, and a host of other contributors to the recent paleontological literature.

AN EXAMPLE: MORPHOLOGIC RATES OF EVOLUTION AND THE TAXIC APPROACH

Simpson (1944:3) defined "rate of evolution . . . as amount of morphological change relative to a standard," and paid relatively less attention to taxonomic rates. In 1953, Simpson made more explicit the distinction between morphologic and taxonomic evolutionary rates and expanded his discussion of the latter. Boucot (1975) in contrast, used the expression "evolutionary rate" solely to mean taxonomic rate (specifically, rate of origin of new brachiopod genera) and this corresponds only to the taxonomic frequency rate subdivision of Simpson's (1953:10) category of taxonomic rates. In the voluminous literature on evolutionary rates, it is usually unclear precisely what kind of evolutionary rate is intended—"genomic" (see Schopf et al., 1975, for a discussion of this type of evolutionary rate and its relationship to paleontology), morphologic, or taxonomic. Although Simpson (1944, 1953) was correct in separating these various kinds of rates and asserting the unique interest attached to each, the tendency not to distinguish among them implies that the fundamental problems underlying such investigations are interrelated, if not identical.

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[2] Lesch (1975) has reviewed the work of Romanes and other evolutionary biologists of the latter half of the nineteenth century who stressed the importance of isolation in the speciation process. That a distinction between the transformational and taxic approaches was evident to Romanes is well illustrated by Lesch, who quotes Romanes (1886:347): "it (i.e., natural selection) is not, strictly speaking, a theory of the origin of species: it is a theory of the origin—or rather of the cumulative development—of adaptations, whether these be morphological, physiological, or psychological, and whether they occur in species only, or likewise in genera, families, orders and classes." Lesch (1975:487) then elucidates: "In other words, while the theory of natural selection has succeeded in accounting for the great central fact of adaptation in nature, it had failed to give a complete explanation of the special phenomena associated with species formation, in particular the splitting up of a single species into two or more distinct species." This issue is an old one in evolutionary biology!

There are, of course, exceptions to the generalization that paleontologists have remained oblivious to the taxic approach. For example, J. M. Clarke (1913:17 ff.), citing the works of Wallace, Wagner, and Jordan, was clearly thinking in "taxic" terms in his analysis of the role of geographic isolation in the development of the Devonian faunas of the southern hemisphere. But such examples are few and far between, and constitute only a muted counterpoint to the main theme of "transformationism" in paleontological research over the past 100 years.

Degree, hence rate, of genetic change has long been known not to be invariably closely correlated with morphologic change. The existence of sibling species (for example, *Drosophila persimilis* and *D. pseudobscura*—see Dobzhansky, 1951:267) when compared with the rampant variation within a single species (for example, *Homo sapiens*) suffices to dramatize this long-known point, as does the recent demonstration (King and Wilson, 1975) of the close genetic similarity between *Pan troglodytes* and *Homo sapiens,* two species which appear to us to be so different. Similarly this point is directly related to degree, hence rate, of morphological change versus speciation rates; a highly speciose group (such as most drosophilid faunas, perhaps excepting Hawaii—see Hardy, 1970:451) may remain morphologically rather uniform, or produce a broad spectrum of morphologically distinctive species (as in African cichlid fish of the genus *Haplochromis*—see Fryer and Iles, 1969). Finally, degree, hence rate, of genetic change is not clearly related to speciation rate (Avise and Ayala, 1975). These various sorts of rates are "decoupled" (*sensu* Stanley, 1975) to some extent, and it is legitimate to investigate each separately.

When we turn to a specific problem involving rates and examine the hypotheses proposed to explain it, the distinction between the transformational approach and the taxic approach becomes relevant. For example, bradytelic lines—defined by Simpson (1953:113) as "low rates" or "arrested evolution"—imply, above all, extremely low rates of morphological evolution over a considerable span of time—usually at least 100 million years. Most studies of bradytelic lines have focused on the question: what are the factors governing this observed slow rate of morphological transformation? The difficulty in applying a purely hypothetico-deductive approach to evolutionary paleontology is nicely exemplified in the set of explanations devised by paleontologists (and others) to explain bradytely. Simpson (1953:319 ff., see also p. 303 ff) summarizes many of them ably, himself believing that bradytelic lines are qualitatively (as well as quantitatively) different from moderate and fast rates, and concluding (1953:334) "bradytelic lines are merely the residuum of a process that regularly reduces the percentage of unchanged groups but that stops short of reduction to zero . . . ."

There seem to be three general "transformation" sets of explanations of bradytely. First, lack of sufficient genetic variability (for a variety of reasons) has been cited (see Selander et al., 1970, and references cited therein) as a major factor. If genetic varibility be the raw stuff of evolution, lack of such variability might be construed as an impediment to change. But Selander et al. (1970) have shown that *Limulus polyphemus,* a surviving member of a classically bradytelic lineage discussed more thoroughly below, is about as polymorphic at a sample of its loci as most other organisms. A second set of explanations involves selection; for example, Simpson (1953:331) asserts that bradytelic lines are not subject to intense (directional) selection pressures, but rather are always under intense stabilizing (centripetal) selection pressure. The final general kind of explanation of bradytely involves adaptation per se—organisms have persisted essentially unchanged because their adaptations were successful, their habitats persisted, their niches remained recognizably the same, hence so did they. This argument is appealing, but amounts to a tautological restatement of the problem—it essentially says that organisms have persisted because they have persisted. There seems to be few avenues to test most of these hypotheses directly.

Fig. 1, taken from Westoll (1949: Fig. 11), is a typical bradytelic curve for rate of character loss within Dipnoi (following an early tachytelic period), compared with the actual number of dipnoan genera given by Romer (1966). The curves are similar:[3] where there is a high rate of morphological change, there tend to be more taxa recognized by systematists. This poses an important conundrum: do lineages undergoing a relatively high rate of morphological transformation appear to be more taxically diverse simply because their greater morphological variety allows us to recognize more taxa within them? Or is it the other way around—are lineages, which exhibit relatively greater amounts of morphologic change, more taxically diverse because they have a higher rate of speciation? If the former is true there is no compelling reason to consider

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[3] Raup and Gould (1974) have illustrated the pitfalls of concocting evolutionary explanations for spindle diagrams of diversity and the lesson is directly applicable to the interpretation of these taxonomic frequency and survivorship curves. Eldredge (1978: Fig. 10) has recently presented a curve of trilobite family diversity which is geometrically very similar to that for Dipnoi (Fig. 1b) and Limulicina (Fig. 2) presented here. Trilobites, as a group, were by no stretch of the imagination bradytelic. Thus, low diversity, on the species or at most the generic level, must be an added element to the very definition of bradytely—see Eldredge, 1975, for a further discussion.

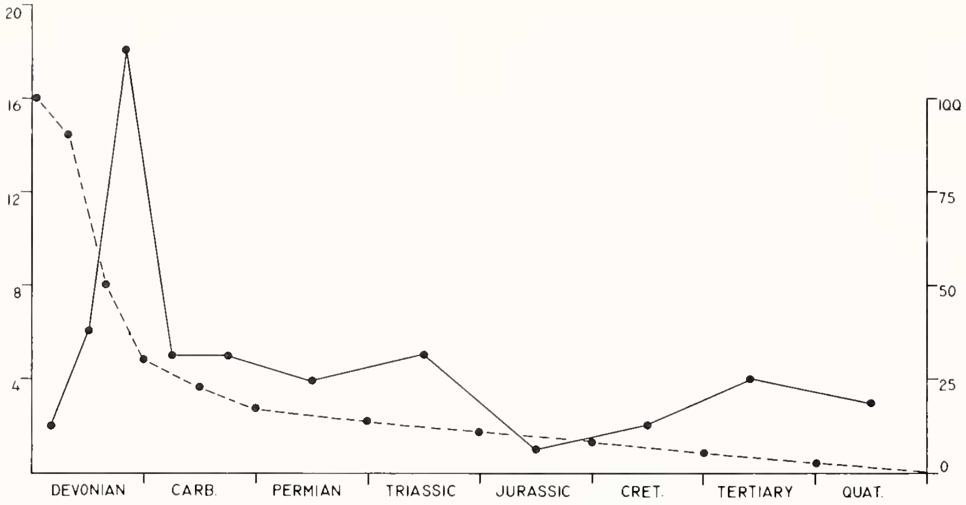

Fig. 1.—Comparison of Westoll's "graph showing rate of loss of characters [for entire body] of the ancestral type during evolution of Dipnoi" (dashed line with scale on right; redrawn from Westoll, 1949: Fig. 11) with a tabulation of dipnoan generic diversity through time tabulated from Romer (1966; solid line with numbers of genera on left). Both diversity and rate of morphological evolution were initially high ("tachytelic"). The bradytelic phase, comprising some 87% of the total history of the group (345 of 395 million years) is accompanied by a greatly reduced but apparently stabilized generic diversity. Compare with Fig. 2.

arguments other than the sort listed above to explain differential rates of morphological change. In that case, it would appear that the problem of bradytely has been exhausted and we are left with a number of narrative, essentially inductive explanatory generalizations (not all mutually exclusive) with which we must be content. However, if we examine the alternative hypothesis, that morphological evolutionary rates reflect, however indirectly, speciation rates, the problem of bradytely takes on an entirely different guise and perhaps admits to a more compelling narrative explanation, and possibly to a more rigorously hypothetico-deductively based investigation.

Fisher's (1975*b*) recent detailed study of the evolution and functional morphology of xiphosurans provides a comprehensive review of the diversity and morphological evolution of the infraorder Limulicina from the Middle Devonian through the Recent. Fig. 2, based on data from Fisher (1975*b*) graphs the approximate number of valid species extant during some part of each third of the various geologic periods. Fisher (1975*a*, 1975*b*) has demonstrated that the classic view of virtually total stasis in limuline evolution has been overstated. For example, Fisher (1975*b*) convincingly shows that the Carboniferous Euproopacea attained full fusion of the opisthosomal segments independently from the true Limulacea. This interpretation is contrary to conventional interpretations (or assumptions) most recently advocated by Eldredge (1974*a*) who cited opisthosomal fusion as a synapomorphy linking the two groups. Fisher (1975*a*) also established actual differences in shape (that is, not just size) of various prosomal and opisthosomal features which bespeak rather more profound differences in behavior among genera of Limulacea. In spite of the enumeration of a large number of morphological differences among the 23 genera and approximately 45 species of living and fossil Limulicina that Fisher has documented, this infraorder remains a typical example of a bradytelic lineage. Fisher (1975*b*) accepts four living species of Limulicina as valid—*Limulus polyphemus*, *Carcinoscorpio rotundatus*, *Tachypleus gigas*, and *Tachypleus tridentatus*. Inspection of Fig. 2 reveals that this low diversity has been characteristic of the infraorder from the Lower Permian through the Recent. The fact that Recent diversity is so similar to the known diversity during this interval suggests that the fossil record is a fairly accurate reflection of the actual diversity, though of course we must expect it to be an underestimation. Thus, this bradytelic lineage is characterized by relatively little morphologic diversity, low rate of morphologic change, and low taxic (species) diversity for all but the earliest phase of the evolution of the Limulicina.

Bradytelic lineages thus exist and their existence remains to be explained. What follows, first, is an attempt to supplant the inductive narratives, which

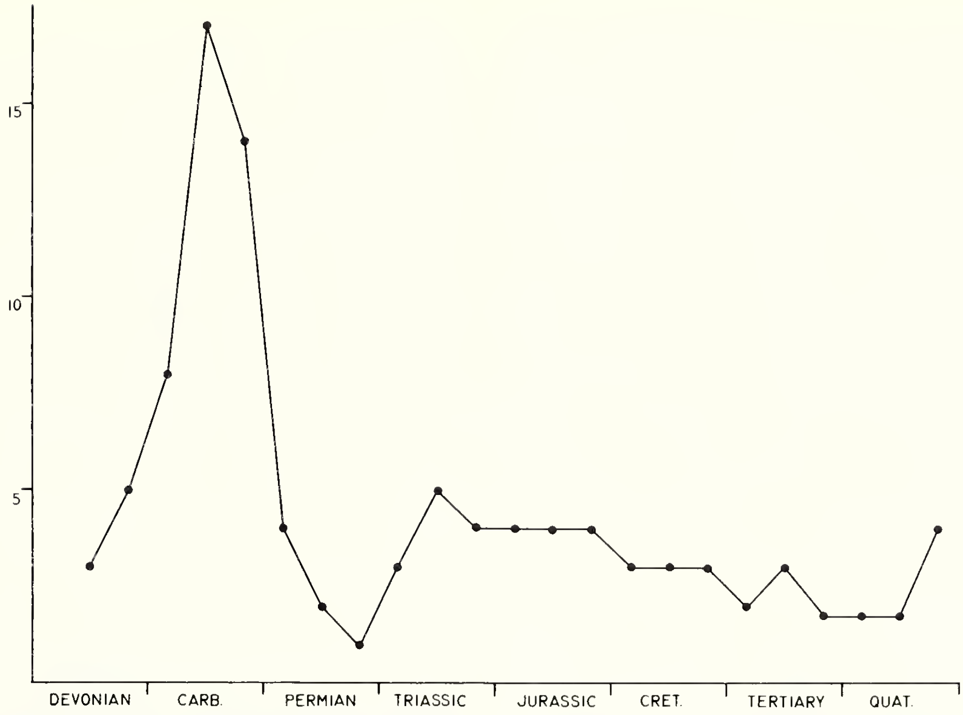

Fig. 2.—Species diversity of Limulicina through time, based on analysis and compilation by Fisher (1975*b*).

approach the problem from a purely transformational standpoint by framing a narrative in the context of taxic evolution. This inductive narrative is then presented as an hypothesis, the components and testability of which will be considered immediately following its presentation.

Assume that very low rates of morphological change are generally correlated with low taxic diversity and that very high rates are correspondingly correlated with high taxic diversity. Counter-examples to these generalizations are easily found; for example, Cambrian echinoderms exhibit substantial morphologic diversity but little taxic diversity (see Sprinkle, 1976 and references therein), whereas North American minnows are speciose and morphologically uniform (Avise and Ayala, 1975, 1976). Nevertheless, insofar as bradytelic lineages are concerned, low rate of morphologic change is correlated with low taxic diversity—compare, for instance, rhynchocephalians versus other diapsid "reptiles," coelacanths and lungfish versus Actinopterygii, Monoplacophora versus Gastropoda, as well as Xiphosura versus both Crustacea and Trilobita.

Inasmuch as the problem of bradytely is being recast in terms of the taxic approach, we consider the possibility that low speciation rates determine the low observed rate of morphologic change, rather than asserting that the low rate of morphologic change results in such little morphologic diversity that systematists do not, or cannot, recognize many discrete taxa. There is the third possibility—that the correlation may be fortuitous and thus low rates of morphologic change may in no way be dependent upon low rates of speciation.

But since we are stating a problem in taxic evolution, we might inquire if there might be a causal connection between speciation rate and degree of morphological change in the evolutionary process. Under orthodox darwinian notions of the significance of evolutionary morphological change, we assume that such change is generally adaptive—morphology is related to ecological niche occupation and exploitation. Similarly, species diversity is related to ecological niche occupation and exploitation, an area of intense investigation among contemporary ecologists, and a theme developed prominently in the recent paleontological literature, notably by Valentine (1973 and elsewhere) and by Bretsky and colleagues (for example, 1970). In view of these relationships, niche theory holds promise for shedding light on aspects (including rates) of the relationship between the evolution of morphology and the evolution of diversity.

How might this work? Organisms can be characterized on a sliding scale of eurytopy-stenotopy as a means of describing specific aspects of an organism's utilization or tolerance of a given habitat parameter. I use these terms explicitly to refer to relative degrees or breadth of such utilization or tolerance, and not as a measure, for example, of the range of specifiable habitats a species may be found in. The concept of eurytopy-stenotopy is largely qualitative and evaluations are generally subjective, though many physiological parameters are easily quantifiable (for example, Bradshaw, 1961, on relative temperature and salinity tolerances of six species of benthonic foraminiferans). There is a further important caveat in such considerations—a species may be stenotopic in one respect, and eurytopic in another; furthermore a species may be stenotopic in one part of its range, life cycle, or season (for example, rely on a single food resource) while quite eurytopic under other conditions. Yet it appears to be valid to distinguish between "basically" eurytopic species (*Limulus polyphemus* being an excellent example) and stenotopes (for example species of *Haplochromis* cited above), in terms of a comparison of feeding and locomotory behavior and ranges of physiological tolerance. To be useful, such comparisons should be made between closely related organisms in comparable environments.

Stenotopic organisms, almost by definition, are specialists narrowly adapted when compared to their closest analogs. Although there would seem to be a limit to resource subdivision (but see Flessa and Levinton, 1975), stenotopes are those species which exploit only a small portion of the resource space theoretically available to species of their general kind. Eurytopes, in contrast, are broadly adapted generalists. Most paleontologists (for example, Bretsky and Lorenz, 1970) have emphasized the implication of these alternative adaptive strategies in terms of ability to survive extinction events. But it might be asked how these different strategies came about in the first place and came to be maintained in the second place.

There are three major possible outcomes to the onset of sympatry of two closely related species (see Mayr, 1963:81, for a discussion): competitive exclusion, hybridization, and accommodation. Accommodation between two species with initially overlapping niches is typically accomplished through resource subdivision, which frequently results from intensification of specializations already begun prior to sympatry—an accentuation of differences already latent in the allopatric state (Eldredge, 1974*b*). Accommodation amounts to a *de facto* generalization of the typical response of stenotopes to interspecific competition—that is, there frequently ensues a further division of resources. Most closely related sympatric species are rather narrowly adapted organisms. Therefore we may hypothesize that stenotopy increases the probability of survival of new species budded off essentially by accidents of changing geography. On the average, taxic diversity has to be higher among stenotopes. Furthermore, ecological specialization also implies, on the average, that behavioral differences among species will ultimately show up as anatomical specializations. Therefore morphological change itself will be more common and more apparent among stenotopes. Because successful speciation will be more common, morphological change should accumulate more rapidly within stenotopic lineages. Again, African cichlids of the genus *Haplochromis* seem to fit this scenario well, and much of the narrative model corresponds very closely to specific conclusions reached by Fryer and Iles (1969) in their analysis of these fish.

The opposite should be true of eurytopes. Eurytopes are generalized in behavior and physiology, and therefore have relatively unspecialized somatic organizations. Eurytopes, furthermore, tend to be far-flung (Jackson, 1974) and tend not to occur sympatrically with closely related species (for example, the largely allopatric distribution of the relatively few species of the eurytopic cichlid *Tilapia* compared with the great amount of sympatry among *Haplochromis* species; Fryer and Iles, 1969)—presumptive evidence that eurytopes competitively exclude, far more often than they accommodate, closely related species. The data pertaining to limuline evolution also fit these generalizations quite closely. It would thus appear that speciation rates within eurytopic lineages are automatically dampened by their ecological strategy, and, as a corollary, morphological change will be retarded. Remembering that rate of morphological change is not directly or fully correlated with speciation rates, it is further relevant that when successful speciation events do take place within eurytopic lineages, the new species themselves tend to be eurytopic, hence remain morphologically unspecialized. Jackson (1974) reaches much the same conclusions for somewhat different reasons.

We may summarize the above inductive narrative as a single hypothesis with several component subhypotheses, all of which were contained in the narrative as assumptions. Thus the single hypothesis is rapid rates of morphologic change are correlated with rapid speciation rates; slow rates of morphologic change are correlated with low speciation rates[4]. Correlation is statistical, and a value of R = 1 is not expected; nor, of course, is the narrative held to be true if this initial hypothesis is rejected. But it may be falsified, though not by pointing to a single counter example (for example, Cambrian echinoderms as cited above), as inviolate laws seem impossible to find in evolutionary biology.

Boucot (1975) has recently amassed an enormous amount of data on mid-Paleozoic brachiopods, concluding that eurytopic genera[5] have relatively long stratigraphic ranges, whereas stenotopes (endemics) have relatively short stratigraphic ranges. The former evolves more slowly than the latter. Boucot's data are taxa, that is, aggregates of individuals that Boucot and many others had previously defined on the basis of observed morphological similarities and differences. Thus, in an important way, Boucot has thoroughly confounded morphological and taxic evolutionary rates—the issue he confronts is rate of morphological change, but the data he uses are of generic diversity, and thus we have in a real sense an independent test of the hypothesis above. Based on Boucot's presentation of the brachiopod data, rapid rates of morphological change are indeed highly correlated with more speciose groups, whereas slower rates of morphological change are highly correlated with less speciose groups. Because the interval of time is the same for all groups examined, "more speciose" means "speciating at a higher rate." Boucot (1975 and manuscript) does not seek a purely taxic (speciational) explanation for the correlation he reports, but his data do serve to corroborate this first hypothesis—a further warning that a large if not infinite number of narratives can be concocted for any given set of observations.

Insofar as the specifics of the competition model are concerned, the above inductive argument is only as good as prior theoretical analysis of empirical data already performed by others. Bock (1970, 1972) has utilized competition theory extensively in his analysis of the adaptive radiation of the Hawaiian honeycreepers and other groups. Bock specifically invokes (divergent) character displacement, which results from sympatric interactions among closely related (hence initially similarly adapted) species, to provide the selection force for the direction of morphological change (and specialization) that his prior analysis of relationships revealed. Studies of competitive interaction involving niche subdivision and divergent character displacement are legion, though their interpretation remains arguable (see Grant, 1972, for a recent review of the literature and a skeptical view of the success of the concept; Eldredge, 1974*b*, summarizes the meager paleontological literature on this subject). The studies by Bock and others tend to corroborate the notion that significant amounts of morphological change take place in conjunction with species interactions. But they tell us nothing about the taxic and morphologic stasis hypothesized to take place when competition results in mutual exclusion.

Stanley (1973) in a lucid paper has utilized competition theory to explain the disparity in taxic rate of evolution of mammals *vis à vis* marine bivales. He concluded that, on the whole, sessile bivales are less competitive *inter se* than are mammals[6]. The argument is appealing. To test the hypothesis advocated here, that eurytopic/stenotopic ecological strategies are the prime determinant of a given species' reaction to sympatric competition with a close relative, it would be more germane to compare relatively faster and more slowly evolving lineages within both the mammals and clams. But for the most part, the model developed herein is closely similar to Stanley's model linking differential rates of taxic evolution with interspecific competition.

How, in fact, do we test the hypothesis—eurytopes react to competition by exclusion, whereas stenotopes tend to subdivide niches (hence interact and undergo divergent character displacement as per above hypothesis)? There are several ways—the first being the familiar demonstration of correlation. Fryer and Iles (1969) reach precisely these conclusions upon comparison of the distributions, morphology, and behavior of the cichlid taxa they studied. In a way the hypothesis merely generalizes an empirical observation long known to ecologists and systematists. A further test of the hypothesis that eurytopes tend to mutual exclusion upon the onset of sympatric competition could be gained from mathematical modelling, particularly via simulation. Studies of this kind specifically addressed to this issue have yet to be performed.

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[4] Stanley (1975:647) has recently graphed the same data on Dipnoi presented here, and has briefly discussed bradytelic rates. He argues that "groups of taxa that have survived at consistently low diversities over long periods of time should exhibit very little evolutionary change," and that in fact living fossils provide a test of the general validity of the "rectangular model" of evolution. Thus our hypotheses on bradytely are identical, apparently because a preference for the taxic approach immediately leads to such a notion. I stop short of citing this coincidence (Eldredge, 1975; Stanley, 1975) as corroboration of the hypothesis itself.

[5] Boucot's criterion for determining eurytopy-stenotopy is basically the relative breadth of geographic distribution of a genus. This criterion was explicitly rejected earlier in this paper, as specialists may be widely distributed and generalists decidedly less so, all according to the distribution of their habitats. Yet the correlation Boucot relies upon seems real enough and, in any case, no other criterion for judging eurytopy-stenotopy with fossils comes readily to mind.

[6] Van Valen (1976) has taken issue with Stanley's evidence, arguments, and conclusion that there is relatively little interspecific competition among clams.

Implicit in the inductive model linking morphological rate of evolution with speciation rates, is the notion that morphological change in evolution is largely effected through speciation. This may be stated in another way—we may test the hypothesis that, once established, species tend not to exhibit much morphological change cumulatively (over time) though they would of course be expected to display geographic variation as well as the effects of sympatric interaction with closely related species should this ever occur. Avise and Ayala (1975) recently tested the rival hypotheses that genetic change within a lineage is correlated with (1) amount of speciation, and (2) time (duration of the lineage). Their results were ambiguous, but if anything favored (2). Vuilleumier (1969) has documented allopatric divergence among closely related species of Andean birds, indicating that phyletic evolution is a real possibility. Given time, selection as well as random sampling effects from generation to generation are expected and observed to lead to cumulative changes in both genotype and phenotype within species[7].

But it is still of interest to investigate the relative importance of phyletic morphological change within a species versus the importance of speciation in effecting that change (via a non-random sampling of the parent species genotype/phenotype and post-speciational interspecific interactions more than any "genetic revolution" that might be imagined to take place at the "moment" of speciation). How do we test the relative contribution of these two factors in effecting morphological change?

Close analysis of low-level (ca. species) taxa in the fossil record may be used to arbitrate the discussion. But the situation is not at all straightforward. Gingerich (1974, 1976) concludes that phyletic change in morphological features is the rule, not the exception within lineages of ancestor-descendant population samples. His procedure is straightforward—select a series of stratigraphically closely spaced samples of specimens which, by prior analysis, are thought to belong to a monophyletic assemblage. Select one or more morphological features and simply document what happens to them up the stratigraphic section. Some characters exhibit change, others do not. Gingerich (1974, 1976) has found that the surface area of M_1 of several different Eocene mammalian taxa exhibit gradual, progressive change (see Gould and Eldredge, 1977, for a specific critique of Gingerich's methodology). Graphing the changes against stratigraphic position, Gingerich then simply encircles segments of lineages most clearly linked continuously, and names taxa on the basis of these clusters. Morphology evolves inexorably, and we chop it up to name taxa. Evolution is phyletic.

Eldredge and Gould (1972) and Eldredge and Tattersall (1975) have argued that the first step in paleontological systematics is to recognize basic taxa. Citing examples from trilobites, gastropods, and hominids, they contend that it is possible to recognize and diagnose species at any one point in time, to distinguish such taxa from others living sympatrically (including synchronically, of course) as well as allopatrically and/or allochronically. It is possible to specify in what respects those species differ among each other and, in most cases, those species-specific *differentia* are found in other samples, be they older, younger, or elsewhere. In other words, species are real entities with both geographic and stratigraphic distributions (few species are known from but a single bedding plane). Temporally, there is no significant change in these species-specific *differentia*—after all, it is this very continuity, which allows us to recognize a species in more than one place at more than one time. Other morphological features within the stratigraphic distribution of a species—features which were not cited as *differentia*—often *do* show sequential change within the history of that species. They conclude that species are distinguished both spatially and temporally by virtue of a number of specifiable attributes, which tend *not* to change inexorably as time goes by. Most morphological change is found to be among-species, hence associated with speciation. Stanley (1975) has called this the "rectangular" model of evolution.

Gingerich's entire methodology, hence conclusion, springs from the transformational approach, whereas those of Eldredge and Gould (1972) and

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[7] It should be noted that the relatively speciose lineage (North American minnows) investigated by Avise and Ayala (1975, 1976) is morphologically uniform. We may still hypothesize that relatively greater amounts of genetic change, when observed, are strongly correlated with relatively high rates of speciation, in common with the hypothesis above linking morphological rates with speciation rates.

Eldredge and Tattersall (1975) derive from the taxic approach. The disagreement among these authors is ultimately derived from starkly different ways of looking at the evolutionary process. The problem lies more in the fundamental assumptions rather than in faulty logic on either part within the framework of the chosen approach. Thus I would conclude that the patterns of morphological change both within and among species in the fossil record provides a crucial test of species stability through time, and thus tends strongly to corroborate the inductive narrative above on evolutionary rates. In the framework of the taxic approach, this may be so. But as long as we retain these two alternative approaches to evolutionary theory, we shall continue to argue issues from different premises, and we may confidently expect to get nowhere.

SUMMARY AND CONCLUSIONS

1) A complete evolutionary theory requires the presence of two distinct components—(a) a theory of mechanics to explain genetic, morphologic, and behavioral change, and (b) a theory pertaining to the origin of species.

2) Many of the classic areas of investigation, especially in paleontology and genetics, emphasize the aspect of evolutionary mechanics (the "transformational" approach) to the point of near exclusion of consideration of the origin of taxa (the "taxic" approach).

3) Integration of the two approaches is best effected by considering the issues of the transformational approach as a subset of those of the taxic approach. This amounts to saying that taxa evolve, not individual organisms or parts thereof.

4) The problem of bradytely ("arrested evolution") is chosen as an example of a topic in evolutionary biology nearly always stated and investigated purely in terms of the "transformational" approach. Previous hypotheses (actually inductive narratives) proposed to explain bradytely include (a) lack of available variability, (b) lack of directional selection and/or presence of strong "centripetal" or "stabilizing" selection, and (c) retention of original adaptation in conjunction with habitat persistence.

5) Restated in taxic terms, a narrative explanation for bradytely is proposed:

a) Bradytelic lineages are characterized by low diversity for the greatest part of their temporal persistence. Therefore, there is a problem in deciding whether diversity is low simply as a result of there being little morphological diversity for a systematist to use to recognize and name taxa, or whether morphological diversity is low because there has been relatively little speciation within the lineage. The narrative proposed under the taxic approach poses the latter possibility.

b) Taxonomic, morphologic, and genetic evolutionary rates are "decoupled" to a significant extent.

c) However, there is evidence that lineages exhibiting truly low rates of morphologic change have low taxic diversity, and that lineages characterized by high rates of morphologic change have high taxic diversity.

d) Eurytopic organisms (ecologic generalists) react to competition with close relatives largely by mutual exclusion, whereas stenotopes tend toward accommodation by specialization and partitioning of resource space.

e) Thus stenotopes have a higher probability of successful speciation and thus behavioral specializations ultimately are expressed in terms of anatomical modifications. Speciation rates of eurytopes are dampened by their ecological strategy and thus their relatively generalized behavior and physiology leads to retention of relatively primitive phenotypes.

6) Several ways of testing the component hypotheses of the narrative are suggested. The problem remains difficult to attack in an hypothetico-deductive manner. Correlation between different parameters (for example, between low rate of morphologic change and low taxic diversity; between degree of sympatric occurrence among congeneric stenotopes versus congeneric eurytopes, and others) offers a means of rejection, though not a particularly strong source for corroboration.

7) Many of the controversies in contemporary evolutionary biology stem not so much from the relative merits of the logic or data used in arguing a particular point of view, but rather from funda-

mentally different approaches taken by the investigators. The current controversy in paleontology over the relative importance of phyletic evolution versus speciation is an excellent case in point. Most adherents of the view that evolution is essentially phyletic see evolution primarily as the cumulative change of gene content, frequency, and expression. The fundamental assumption of the opponents of this view appears to be that evolution is quintessentially the origin of new taxa (species). Thus the two opposing views (that is, on the relative importance of phyletic evolution versus speciation) are not sufficiently comparable to allow rejection of one in favor of the other. The argument is, in the end, over which approach to evolutionary theory is the more appropriate. The taxic approach seems the superior of the two because of its capacity for subsuming the transformational approach. The converse does not appear to be true.

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THE SYNTHETIC EXPLANATION OF MACROEVOLUTIONARY CHANGE—A REDUCTIONISTIC APPROACH

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INTRODUCTION

Formulation of the synthetic theory of evolution began in the early 1930's with the high hopes of explaining all evolutionary phenomena with a single unified theory. Many of the hopes of these evolutionary biologists were realized, some more than they had dared to believe possible. Other facets of evolutionary theory, once considered incontestably established, were subsequently questioned. Yet the single aspect of evolutionary biology that eluded attempts for successful and convincing explanation is macroevolution—the appearance and subsequent specialization of distinctive new features and taxa. Advocates of the synthetic theory assumed, largely as untested conviction, that major evolutionary changes were simply the consequence of many small modifications and that these large changes would be understood if the microevolutionary events were fully comprehended. Although I believe that this assumption is correct and will advocate it in this paper, one of the major failures of the synthetic theory has been to provide a detailed and coherent explanation of macroevolution based on the known principles of microevolution. In spite of the beliefs of the advocates of the synthetic theory, macroevolution has not been reduced successfully to microevolution.

Because of this failure of the synthetic theory, two major explanations have been advocated for major evolutionary modifications. One is the reductionistic theory as mentioned above and which will be advocated herein. The other stems from the period of idealistic morphology of the second half of the nineteenth century with strong pre-Darwinian roots, and can be termed as the quantum or saltation theory. Differences between these two conflicting theories, as well as the confusing complex of ideas associated with macroevolutionary explanation, are demonstrated by two recent textbooks of evolution published by the same house. Dobzhansky et al. (1977) advocate strongly the synthetic view with a firm statement that macroevolutionary change must be adaptive throughout. Grant (1977) leans strongly toward the quantum theory of major evolutionary change although he rejects extreme versions of saltation. Yet both texts rely heavily on the ideas of Simpson (1944, 1953) and both cite my analysis (Bock, 1970) of the evolution of the Hawaiian honeycreepers (Drepanididae) as an example of adaptive radiation.

I would like, in this paper, to provide a detailed reductionistic explanation of macroevolution within the tradition of the synthetic theory. An important part of this analysis will be an examination of the role of the species and of speciation in this explanation. At this point, I would like to acknowledge my debt to my teacher and mentor Ernst Mayr whose name is usually associated with the species concept and speciation, but who has done more to establish the foundations of an explanation of macroevolutionary phenomena than any other living evolutionist.

LIMITS OF MACROEVOLUTION

Before a causal theory of macroevolution can be postulated, it is necessary to establish the limits of this type of evolutionary change and to distinguish it from microevolutionary phenomena. Unfortunately no definite boundary can be drawn between macro- and microevolutionary changes; I believe that the two grade smoothly into one another. Yet even when no sharp demarkation can be established between two concepts or phenomena, such as night and day, frequently the two may be easily recognized. Hence, by microevolutionary change, I mean those modifications of the level studied by population geneticists and by animal and plant breeders. These would be differences of the degree that distinguish populations and subspecies of the same species or that distinguish congeneric species.

Microevolutionary events are ones amenable to experimentation and direct observation. Macroevolutionary changes are those modifications of the level studied by comparative anatomists and paleontologists. They would be differences of the degree that separate families, orders, and groups of higher categorical rank. Differences between genera are usually considered to be at the lower end of the scale of major evolutionary change. The origin of a distinctive new feature, such as the vertebrate eye or the mammalian jaw articulation, or the radical modification of an existing feature, such as the evolution of the tetrapod limb from a crossopterygian fin or the avian wing from a reptilian forelimb, would all be major changes. Macroevolutionary changes are usually not open to experimentation or direct observation, although some of the results of animal and plant breeding, for example, the fancy breeds of goldfish and the diverse breeds of dogs, surely must be regarded as major modifications.

I do not want to accept any level as the demarcation between micro- and macroevolution in a hard and fast way. Successful development of the reductionistic explanation of major evolutionary change is not dependent upon any particular limit between these two degrees of evolutionary change. More important is the continuum between these facets of evolutionary change and the fact that examples of the two types overlap rather broadly.

REDUCTIONISM

One of the central arguments about theories of the mechanisms of macroevolution is whether they are reducible to mechanisms of microevolution. Stanley (1975) states that macroevolution is not reducible to microevolution and I claim that it is. This is one of the fundamental distinctions between quantum and synthetic theories of major evolutionary change. A consequence of these two positions is that in the reductionistic synthetic approach, no mechanisms of evolutionary change need be proposed other than those needed to explain microevolutionary events. In the nonreductionistic quantum approach, at least one additional mechanism of evolutionary change unique to macroevolutionary events must be postulated over and above those needed to explain the microevolutionary phenomena. The additional major evolutionary mechanism(s) must first be postulated and then tested somehow by observations. Moreover, it must be shown that these unique macroevolutionary mechanisms are really not reducible to known microevolutionary mechanisms.

Before this conflict on the reduction of major evolutionary explanation can be solved, it is necessary to clarify the meaning and usage of the concept of reduction of scientific theories. I accept the approach to reductionism advocated by Ernest Nagel (1961; Chapter 11). Reductionism can be interscience or intrascience; we are here concerned with an intrascience reductionism because we remain within the limits of evolutionary biology. The question is whether a large change in evolution is simply the consequence of a cumulative series of small changes and hence explainable by the mechanisms governing the small changes, or whether the large change involves at least one step different from the microevolutionary changes. If the former is correct, then the explanation must include consideration of levels of organization, which is intimately associated with the concept of reductionism.

Nagel argues that reduction of theories to be successful must follow a rigid set of rules. Both the theory to be reduced and the reducing theory must be carefully stated. It is not sufficient to claim that macroevolutionary explanation can or cannot be reduced to microevolutionary explanation. One must state the details of macroevolution—the theory to be reduced—and the details of microevolutionary explanation—the reducing theory. Hence the statements by many advocates of the synthetic theory that major evolutionary change can be explained by the mechanisms of microevolution is correct, but grossly inadequate. Such a statement can neither be defended or argued against because of its vagueness.

The second point mentioned by Nagel is that all phenomena explained by the reduced theory must be explained by the reducing theory for a successful reduction. If there are any phenomena that were explained by the reduced theory that cannot be explained by the reducing theory, then some additional theory is needed and the reduction is not successful. Nagel goes on to argue that for strong reduction all parts of the reduced theory must be derivable from the reducing theory. This requirement is not essential for weak reduction.

The usefulness of reduction of theories is a matter quite apart from whether a particular theory is reducible to another. It is generally accepted that reduction will be useful if the reducing theory can explain many phenomena other than those covered by the reduced theory and if the outcome of the reduction is a more generalized theory uniting many aspects of the particular science or sciences.

Reductionism, especially intrascience reductionism, is closely associated with levels of organization and with the question of the emergence of new properties with increasing levels of organization. It is not clear whether the contrast of microevolution and macroevolution fits into the typical pattern of hierarchical organization, but it does fit many of the characteristics of this pattern. Nagel shows that the common statement that the ''whole is greater than the sum of its parts'' is dependent upon knowing how to add the component parts and whether the details of organization must be included in the addition.

In consideration of whether macroevolutionary explanation is reducible to microevolutionary mechanisms, an important factor is how the individual small steps are added together to obtain a single major change. It is obvious that this addition must be done in a particular manner. The small steps cannot be added randomly or together in a single unit. Rather they must be added sequentially in a chronological series. Thus, the change at any point in time sets the stage for the next change and so forth. Features that arise or are modified at one point in time provide the foundation for the next evolutionary change in features. Macroevolution is thus not just a summation of many small changes, but a sequential summation of many small changes added together in their exact chronological series.

Special care will be given below to stating precisely and completely macroevolutionary explanation as the theory to be reduced and microevolutionary explanation as the reducing theory. Moreover, care will be given to providing reference to the observational and experimental bases used to test the microevolutionary explanation. Attention will also be given to the proper sequential summation of the small changes that add up to a major evolutionary modification. Lack of attention to these facets of reductionism in the past has been a major failure on the part of advocates of the synthetic theory as well as of the quantum theory of macroevolution.

THEORIES AND THEIR TESTING

To be successful, theories or explanation of major evolutionary change must satisfy two major requirements. They must provide a causal explanation of the phenomena associated with large scale modifications and they must be testable against observations. I would like to consider each in turn.

A theory explaining macroevolutionary change, be it the origin and specialization of new features or the adaptive radiation of a new taxon, is a causal explanation similar to theories of speciation, adaptive modification, generation of new genetical variation, and others. Although the time period involved with major changes and hence in the explanation may be great, covering tens of thousands or even millions of years, the theory is not a historical explanation. I am not concerned with analyzing and explaining the evolutionary aspects of a particular feature or of a particular taxon. Rather, I wish to present a causal explanation of macroevolution, which can be used in historical explanations of individual cases.

The fact that a causal explanation of macroevolution includes a sequential analysis of steps does not make it a historical analysis. Numerous other causal explanations, for example, geographical speciation, depend upon a sequence of events arranged in proper chronological order.

The second point is that any successful causal explanation of macroevolution, being a scientific theory, must be tested against experiments and observations. Formulation of any explanation brings with it the obligation of demonstrating how the theory is to be tested and if possible to provide some tests. Development of an explanation that depends upon a vague or untestable mechanism weakens that theory considerably. Perhaps the greatest weakness of past attempts to provide explanations, be they synthetic or quantum, of macroevolution has been the failure to formulate convincing testing procedures. Procedures are frequently proposed to test theories of macroevolution, but upon close scrutiny, these tests prove to be inadequate. An example is the tests of the theory of punctuated equilibria by the fossil record (Gould and Eldredge, 1977: 120). The nature of the fossil record, especially the scale of resolution of time and geographic distribution, is simply inadequate to distinguish between punctuated equilibria and conflicting theories.

Testing of macroevolutionary theories depends upon formulating a proper argument-chain of predications, secondary theories, and connecting links, and finally the experiments and observations serving as empirical tests. It is generally accepted that theories of major evolutionary change cannot be tested directly against experiments and observation. This is generally valid, but we may have far more evidence available from experimental work and from observations of animal and plant breeders than generally suspected.

Special care will be given to outlining the procedures for testing the synthetic theory of macroevolution. The steps in the argument-chain, the secondary hypotheses, the basic links, and the final observations will all be clarified. What types of observations that can and cannot be used to test this explanation will be pointed out.

CONFLICTING EXPLANATIONS OF MACROEVOLUTION

Introduction

Numerous theories have been advocated to explain the phenomena of major evolutionary modifications. All of these need not be discussed because most have not attracted much attention. I will concentrate only upon the two major sets, which are in direct conflict with each other. Although considerable variation exists between the individual theories included in each of these sets, the basic agreements are more important. The first set is that of quantum theories, which are characterized by advocating a single-step jump or saltation at some point in the major change. The evolutionary mechanism involved in this jump is one other than adaptive change under the control of natural selection arising from the external environment. The second set is that of synthetic theories in which the explanation of major changes is reduced to mechanisms acting on the microevolutionary level. These theories exclude any distinctive saltations, do not invoke any special mechanisms of evolutionary change other than those operating at the microevolutionary level, and depend upon adaptive change throughout. All change is under the control of selection arising from the external environment.

Quantum Theories

I will discuss only those quantum theories advocated since the origins of the synthetic theory of evolution in the early 1930's. However, it should be emphasized that the history of ideas of quantum evolutionary changes date back to the period of idealistic morphology in the second half of the nineteenth century and have their roots in pre-Darwinian typology.

By a quantum theory, I mean one that depends upon a single saltation of a magnitude greater than the evolutionary change observed in microevolutionary modifications as studied by animal and plant breeders and by populations geneticists. The mechanism controlling this saltatory jump is either a nonselective one (not natural selection arising from the external environment) or a type of selection distinctive from natural selection. Frequently these theories depend upon the existence of a threshold or of a selective bottleneck.

The concept of typogenesis or typostrophism of Schindewolf (1936, 1950:206) is a clear consequence of the concepts of typology and the idea of "bauplan" of groups developed directly from the concepts of idealistic morphology (Bock and von Wahlert, 1963; Reif, 1975). This theory depends upon the concept that the characteristics of a taxon are expressed in its bauplan or type, that a type boundary delimits a group and that a distinct gap separates the bauplan of one group from that of another. Hence the evolutionary change from one bauplan to another must be a jump over this gap—over the type boundary of one group to that of another. This change must be of a different type than the evolutionary change within the limits of a bauplan. Otherwise there could not have been a type jump. The saltation is not an adaptive change controlled by selection; it is left as a vague evolutionary mechanism.

A similar theory is offered by Goldschmidt (1940:184–395). He argues that the small genetical changes studied by geneticists are insufficient to result in a major change even if many are added together. Rather he suggests that the large changes result from the occurrence of systemic mutations (=macromutations) leading to a new type of organism that is adapted to a new set of environmental conditions. These organisms resulting from systemic mutations have been dubbed "hopeful monsters" by other workers. The role of selection in Goldschmidt's theory is vague. He says (p. 396) that accumulation of micromutants by selection has been "ruled out," and that selection can act on the new form after the systemic mutation. But he nowhere discusses the magnitude of the modifications resulting from the systemic mutations and what are the environmental changes that can act as selection. In the absence of details on this point, it cannot be assumed that the selection discussed by Goldschmidt corresponds to selection acting on microgenetical changes or that it can be related to environments in the real world. It is interesting that Goldschmidt cites the Drepanididae (1940:214–215) as an example supporting his concept of macromutation by systemic mutations, but omits many of the details of geographic variation in species as well as possible intermediate stages represented by extant species.

The concept of "quantum evolution" was developed by Simpson (1944:206–217) and has been widely cited as the synthetic theory explanation of macroevolution in sharp contrast to ideas of typogenesis and systemic mutations. However, careful reading of Simpson's text reveals that his concepts are basically more similar to those of earlier saltatory theories than to a reductionary synthetic explanation of macroevolution. Quantum evolution depends upon a shift of a phyletic lineage through "discontinuities or essentially instable ecological zones" that lie between major adaptive zones. The start of quantum evolution is an inadaptive phase when the lineage enters the discontinuity. Exactly what is meant by "an inadaptive phase," how long it exists and whether selection is acting during this period is not clear. The only conclusion that can be reached is that selection is not acting during the "inadaptive phase" otherwise this phase can not be so considered. The instable ecological zone is regarded as a threshold through which the phyletic lineage must pass quickly or become extinct. These ideas are repeated by Simpson in his later book (1953:389–393) but with some changes. He says that "populations making a quantum shift do not lose adaptation" and "that the direction of the change is adaptive" (p. 391) but later says that "No intermediate stage persisted, because intermediate stages were less efficient (i.e., *relatively* inadaptive)" (p. 392). If these shifts were fully adaptive, then it is not clear what is the distinction between quantum evolution and regular phyletic evolution.

The concept of quantum evolution as expressed by Simpson involves a period where selection is not acting, depends upon passing over a threshold in the intermediate unstable ecological zone, and involves (always?) a key mutation. These expressions sound very similar to the concepts of Schinderwolf and of Goldschmidt in spite of differences in wording. Many of the concepts, such as the inadaptive phase and the ecologically unstable zone, are left vague and unconnected to natural phenomena. Quantum evolution is discussed as an evolutionary mechanism, yet it is not tested nor are testing procedures clearly indicated.

The concept of punctuated equilibria was postulated by Eldredge (1971) and developed more fully by Eldredge and Gould (1972) and discussed again by Gould and Eldredge (1977, see for references to other papers). They wished to examine the concept of slow evolutionary rates as the primary mode of evolution and to introduce the concept of allopatric speciation into paleontological thinking. Certainly the role of speciation has been neglected (although not totally) in discussions of macroevolutionary change and clearly many, probably most, major evolutionary modifications are more rapid than believed by many workers. These concepts were already discussed by Simpson (1944, 1953) and were a central part of my earlier analysis (Bock, 1970) of the role of microevolutionary events in macroevolution. Unfortunately, in the formulation of their concept of punctuated equilibria, Eldredge and Gould shifted from considering whether slow changes were the only or predominate mode of phyletic change to discussing mechanisms of evolutionary change. The result was a series of assertions which makes their concept one of quantum evolution and hence unacceptable.

The major problem is that the concept of phyletic gradualism (the term for slow uniform rate of evolutionary change) has been synonymized for phyletic evolution. This is shown in Eldredge (1971:156–157) and clearly in Eldredge and Gould (1972:87–90; by the equating of Kellogg's [1975] discussion of phyletic evolution with phyletic gradualism, pp. 126–128; and by their statement in the abstract "If, as we predict, the punctuational tempo is prevalent, then speciation—not phyletic evolution—must be the dominant mode of evolution." p. 115). Part of this problem may arise from a combination of their considerations of phyletic speciation, multiplication of species (geographic speciation) and phyletic evolution (1972) where discussions of phyletic evolution and phyletic speciation appear to be interwoven. The consequence is that when they argue against (to the point of denying) phyletic gradualism as a dominant mode of evolution, they do the same for phyletic evolution.

The outcome of this confusion of two concepts, which are completely independent of one another, is that they must reject the synthetic (reductionistic) explanation of macroevolution (for example, Gould and Eldredge, 1977:139–145). They accept the argument of Stanley (1975), which is developed directly from their concept of punctuated equilibrium. Stanley proposes a "rectangular model" for major evolutionary change in which the speciation shifts are regarded to be absolutely different from the evolutionary changes between successive speciations. He introduces a new evolutionary mechanism "species selection," which is not described in sufficient detail and for which no procedures are provided for testing. Stanley states in his discussion (1975:650) that "The reductionist view that evolution can ultimately be understood in terms of genetics and molecular biology is clearly in error. We must turn not to population genetic studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that governs the general course of evolution."

Thus, the concept of punctuated equilibria can be summarized as major evolutionary changes that are the consequence of a series of speciation, not phyletic evolution, in which the mechanism of species selection is important. Further, the explanation of these macroevolutionary changes cannot be reduced to the evolutionary mechanisms operating at the microevolutionary level. Illustration of this change by a rectangular diagram underscores the quantum nature of this explanation. Further, Gould (1977*a*, 1977*b*, 1977*c*) clearly relates the ideas advocated in punctuated equilibria with Goldschmidt's concept of systemic mutations.

A curious approach to quantum evolution has been developed as an outcome of mathematical topological theory of catastrophe (Thom, 1975; Dobson, 1975; Zeeman, 1976; Dobson and Hallan, 1977) developed by Rene Thom. Sussmann (1976) has presented arguments against the implications of this theory as developed in the above cited papers, and Kolata (1977) has commented on this development (see also letters to the editor, 1977, Science, 196:1268–1270). This explanation can be discounted at this time because the possible evolutionary correlations to the mathematical theory have not been worked out, but it is of interest because it demonstrates how attractive the idea of quantum evolutionary steps is to many workers.

Frazzetta (1970, 1975) discussed major evolutionary change from the viewpoint of a functional morphologist, one of the few to do so. Although he does not deny the possibility of major changes resulting from a series of small evolutionary modifications, he believes that macroevolution can also occur by other processes, possibly by the appearance of systemic mutations as advocated by Goldschmidt. Many of the points discussed by Frazzetta, such as the need to examine interactions between structures and the importance of somatic modifications (= physiological adaptation), are important and have been ignored by most evolutionists. As stressed by Frazzetta, analysis of evolutionary modification of morphological systems is far more complicated than appreciated by most workers advocating macroevolutionary explanation. Yet I am not convinced that he presents a compelling argument why all macroevolutionary explanation cannot be reduced to microevolutionary explanation, albeit the microevolutionary explanation will be more complex than usually assumed.

A central issue in several recent quantum theories of macroevolution is rapid speciation in which most of the evolutionary change takes place prior to the complete development of intrinsic isolating mechanisms and the sympatry of the newly appeared species. This factor is critical, for example, to the theory of punctuated equilibria. Carson's (1975) ideas on the genetics of speciation have been cited in this connection. He argues that "microevolutionary events that lead to adaptations, however, do not appear to yield new species as a necessary or even a directly correlated consequence of the adaptation process" (p. 83). Carson suggests that the genetical system of a species is divided into two parts, the open and the closed. The open system responds readily to selection and is the portion of the genotype that has been studied by geneticists. The closed system is not affected by selection under usual conditions and does not yield easily to Mendelian analysis. Under normal circumstances, gene flow does not affect the closed system. Rather, the closed system is modified during speciation with a forced reorganization of the closed variability system by a series of catastrophic stochastic genetic events. This occurs during a period when selection is not acting with a resulting population flush and crash (see his Fig. 2, p. 89). After the crash, a few founder individuals are left from which the new population is generated under natural selection.

Carson is vague on the possible duration of this period of no selection nor does he give reasons to justify the existence of such periods. He does not postulate any new evolutionary mechanisms as the stochastic genetic events occur by known mechanisms of crossing over and other types of genetic recombination. Yet he is vague on why such events cannot take place during periods of normal selection. Because it includes a period of no selection, Carson's concept of speciation belongs to the class of quantum theories and has to be so used (for example, Gould and Eldredge, 1977).

The major difficulty with the theory proposed by Carson is that he does not stipulate how the concept of the closed variability system and the mechanism of its change can be tested by empirical observations. Also, the procedures by which this concept can be tested are difficult to envision because of the stipulation that the closed genetic system is not affected by selection during normal conditions, but changes only during speciation and because of the claim that speciation occurs only as a result of an alteration in the closed genetic system. These interlocking claims form a closed circularity devoid of any means of test by independent observation.

Non-Darwinian evolution as postulated by King and Jukes (1969) and other workers has been invoked by advocates of quantum explanation of macroevolution. Although the theory of non-Darwinian evolution is not a quantum theory, it shares with these theories the notion of a mechanism directing evolutionary modification that is nonselective. Unfortunately, details of the causal mechanism for this nonselective change have been left vague and certainly have not been tested. Other workers in biochemical evolution (for example, Goodman et al., 1975; Goodman, 1976) have argued against the claim of non-Darwinian evolution and state that evolutionary changes in proteins can be explained by selection.

Another theory which does not belong to the class of quantum theories, but should be mentioned here is that of internal selection (Stebbins, 1974:123; Gutmann, 1977:645; Dullemeijer, 1974; Dullemeijer and Barel, 1977). This concept can be interpreted as a form of selection arising from the internal environment of the organism separately and independently of natural selection arising from the external environment. Such a concept has not been clearly formulated nor properly tested. Moreover, the interpretation of a selection independent of natural selection arising from the external environment may not be the intent of Gutmann (personal communication) and possibly not of the other workers. Rather, the concept of internal selection refers to the interrelationships and interactions between features of an individual organism, including all of the mechanisms that serve to keep these features in proper functional balance with one another as required in a viable organism. The various mechanisms on internal adjustment of somatic features and their role in evolution have been considered by few workers (for example, Bock and von Wahlert, 1965; Frazzetta, 1975; Gutmann, 1977) but it is clear that these factors are of prime significance to major evolutionary modification. It is incorrect, however, to term these mechanisms of internal adjustment as internal selection or to imply that these mechanisms are not under the control of natural selection.

Although the emphasis and the mechanisms differ in the above cited and other quantum explanations of macroevolution, the same thread of ideas runs through all. Most important is that they involve a jump or discontinuity at some point, usually during the presympatric phase of speciation, in which a break occurs in the adaptive modification of features and hence of the population. This break coincides with a period in which natural selection resulting from the interaction of the external environment with the organism is not operating. The length of this period is not specified. Often evolutionary modification during this saltation is claimed to be under the control of a nonselective evolutionary mechanism, but this mechanism is not outlined clearly and/or not tested against empirical observations.

These theories fail, in my opinion, for several reasons. The major one is that the needed evolutionary mechanism is not described clearly, or tested; sometimes the indicated mechanism appears incapable of proper testing. Support for the claimed period of no selection is not provided. Although most advocates of quantum theories claim, often tacitly, that macroevolution cannot be reduced to microevolutionary mechanisms, they do not provide the needed support for this claim. To say that macroevolution is or is not reducible to microevolution is not sufficient; the claim must be documented. Most of the quantum theories do not consider the need to decompose major evolutionary changes into a proper chronological sequence of steps and to show how these individual steps are summarized; rather the component parts of a macroevolutionary modification, if considered at all, are usually treated in some unordered fashion. Lastly, macroevolution usually involves modifications of structural features of organisms. Yet most of the discussions of quantum changes exclude consideration of the total biology of these structural features, for example, functional and ecological morphology, and the details of the complex interactions involved in the internal adjustment of somatic features.

Synthetic Theories

The synthetic or reductionistic explanation of macroevolutionary change is based on the postulate that all major evolutionary modifications in features and taxa are fully understandable in terms of evolutionary mechanisms at the microevolutionary level. No new causal evolutionary mechanisms are needed. Large scale modifications are adaptive throughout in that the entire shift is under the control of natural selection arising from the external environment and acting on individuals of the evolving population. Thus, evolutionary phenomena, from the smallest to the largest changes, can be explained by the same unified theory of evolution. This is the basic belief of many evolutionary biologists since the early 1930's, but close reading of most authors reveals that their statements were unsupported statements—articles of faith. Quite probably these repeated unsatisfactory explanations provided the impetus for repeated formulation of alternative, usually quantum, theories.

Macroevolutionary modifications in features and in taxa are those of a general magnitude characterized by difference, expressed taxonomically, of the generic level or higher. Thus, the appearance of a new bone, a new articulation, feathers or hair, modifications in the feeding apparatus to permit taking of different food and many others, would all be major evolutionary changes. As stated earlier, the minimum level of major evolutionary modification is not essential to the discussion. Most workers would place it at a level of difference greater than that observed between genera, others use a level greater than that between species, and still others would accept species level differences as the minimum macroevolutionary change. The synthetic argument to be developed below could be applied equally well whatever level is accepted.

Explanation of all macroevolutionary phenomena is fully reducible, in the strictest sense, to the known mechanisms of evolutionary change at the microevolutionary level. To be specific, these microevolutionary mechanisms are:

a) Those of phyletic evolution, which are two mechanisms acting simultaneously (that is, every generation) and are namely—the production of genetically based phenotypic variation and natural selection arising from the interaction between the organism and the external environment. These are the mechanisms of evolutionary change in populations, which have been studied by populational geneticists (for example, Dobzhansky, 1970, and earlier) and by animal and plant breeders. These are the evolutionary mechanisms that can be tested directly by experiments and by direct observations of known phyletic changes, for example, the history of breeds of dogs, pigeons, goldfish, wheat, corn and a host of other forms of domesticated plants and animals.

b) The mechanisms of speciation—the multiplication of species—as discussed by Mayr (1942, 1963) and many other workers.

Clearly, much disagreement exists on many aspects of these evolutionary mechanisms and it would be necessary to specify exactly which concept one accepts. There are, for example, a number of concepts of geographical speciation (for example, Carson's concept of the closed variability system and its alteration during speciation), which I do not accept. Much argument exists on the extent and role of gene flow. But these disagreements do not affect the claim about reduction of macroevolutionary explanation made above.

Proper explanation of macroevolution events depends upon correct chronological summation of the individual small modification. If this summation is not done properly, then the remainder of the explanation will dissipate.

I must emphasize that macroevolution is viewed as a sequence of microevolutionary events, not as a sequence of species level changes. The latter implies a distinction between evolution at the species level and evolution above the species level or transspecific evolution which I reject. Such a distinction would suggest that phyletic evolution would transcend the species boundary, which is erroneous (see below). The term "transspecific evolution" should be dropped.

The entire period of major change is adaptive, being under the control of natural selection at all times. No periods of inadaptiveness exist nor do any periods exist in which natural selection does not operate. However, the synthetic theory does not specify that all evolutionary change of all individual features must be adaptive. Clearly nonadaptive evolutionary modifications of individual features occur as a result of pleiotrophic relationships between features. Such change may be quite common and indeed is responsible for the evolution of a whole class of features, namely the evolution of intrinsic isolating mechanisms. The only exceptions to the generalization that phyletic evolution of a single lineage must be adaptive (under the control of natural selection) are those modifications associated with founders as proposed by Mayr (1942). However, these changes would be of minor magnitude and would soon come under the control of natural selection. It is improbable to a vanishing degree that the whole or a major part of the phenotypic shift in a macroevolutionary change results from genetic drift.

The synthetic theory does not specify rates of evolutionary change. Certainly there is no upper limit on the rate of change other than that imposed by no rates of microevolutionary modification. And these rates of change can vary with periods of rapid modification intermeshed with periods of low change. Almost certainly rates of major change can be far faster than generally believed and the rates during the origin and early development of a major feature or new taxon are rapid, followed by much slower rates, but these ideas are not new, having been expressed by Simpson (1944). Nor am I in disagreement with the ideas of Eldredge and Gould on rates of evolutionary change expressed in their concept of punctuated equilibria. Arguments on rates of macroevolutionary change are independent to a large degree of the mechanisms of change responsible for these rates.

SPECIES AND PHYLETIC LINEAGES

The species and its evolution is central to the dispute between the several major theories of macroevolution. I will consider only species in sexually reproducing organisms and accept the biological species concept as advocated by Mayr (1942, 1963:19). A *species* is composed of groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. The reproductive gap between species is central and related to preservation of coadaptive complexes of genes. Thus, the species is a genetical unit and an ecological unit with its members forming a reproductive community that shares a common environment. Intrinsic isolating mechanisms serve to preserve the integrity of each species with respect to other sympatric species.

The species concept is most objective as a nondimensional rather than a multidimensional concept (Mayr, 1963:17–19). Thus, sympatric species are most objective with clear-cut limits and separations from one another. As one progresses geographically and chronologically further and further away from a single point, the species distinctiveness becomes more and more vague. Hence, sympatric species are distinct, but allopatric forms become increasingly indistinct with the extreme case being ring species in which the two terminal forms overlap and coexist as species without interbreeding. The unity of the species, which is held together by a common gene pool (and gene flow) and by a similar ecological interrelationship, breaks down as the populations are separated by greater and greater geographical distances and more and more ecogeographical barriers (Fig. 1). A similar breakdown occurs in the unity of the species as one traces it chronologically, generation by generation both forwards and backwards, from a particular point in time. A species comprised of a series of interbreeding populations today is simply not the same as its ancestor 100 generations ago.

The biological species concept is a nondimensional one, but is often applied multidimensionally over a broader geographical space and over a longer temporal period for practical purposes. Thus, I reject the concept of phyletic species except for practical uses in paleontology. The use of the species concept by most phylogenetic systematists as the phyletic segment from one speciation (splitting point) to the next is simply not the same as the biological species concept.

A *phyletic lineage* is the temporal continuum formed by a species (a group of actually or potentially interbreeding populations) reproducing itself generation by generation through time (Fig. 2). A phyletic lineage may remain as a single lineage over long periods of time or it may split into two or more

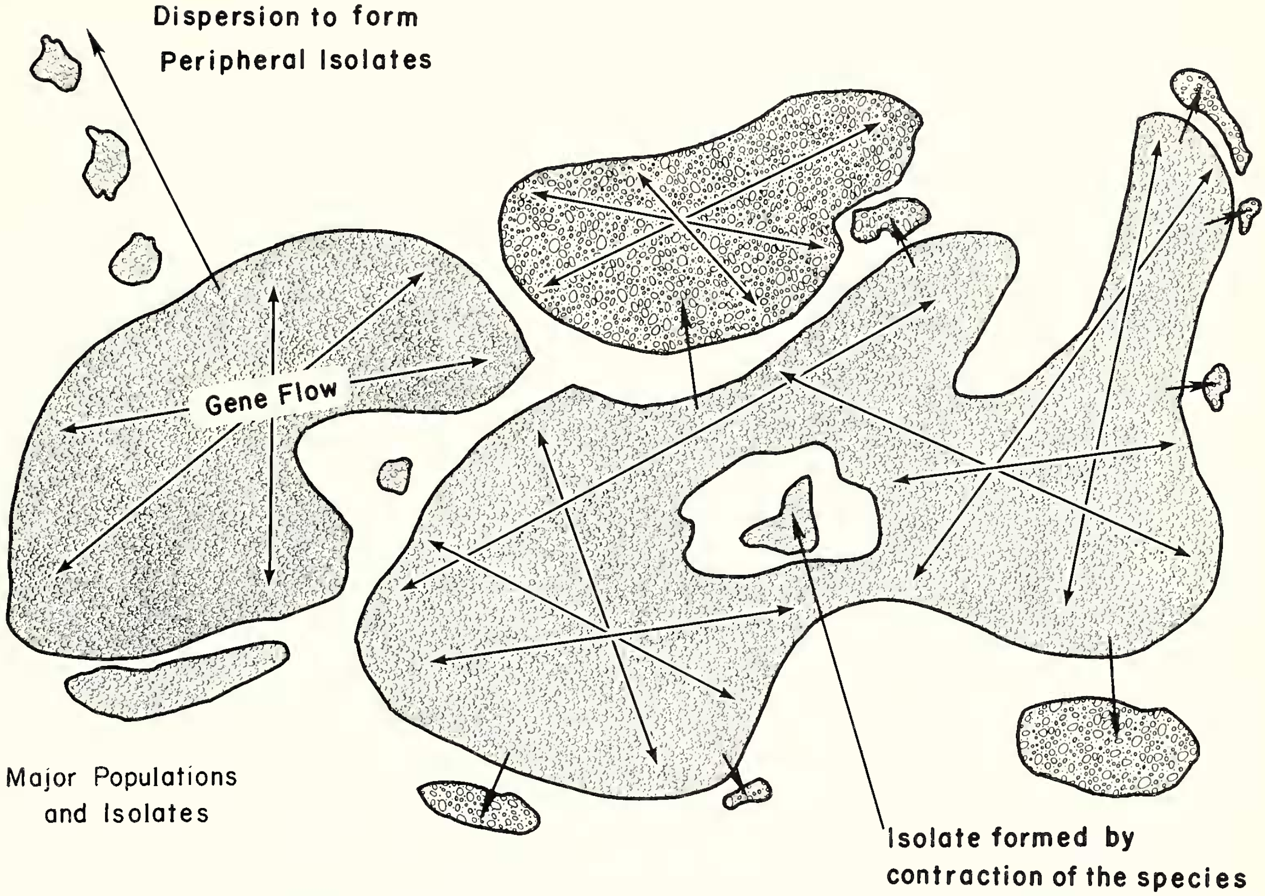


Fig. 1.—Schematic diagram to illustrate the geographic range of a species with several large main populations and a number of small isolates. Some of the peripheral populations were formed by dispersion (indicated by arrows) and perhaps developed from a few founder individuals. Other populations resulted from contraction of the species. Gene flow within populations is indicated by the criss-crossing arrows.

different lineages (= speciate) from time to time. The phenotypic characteristics of the members of a phyletic lineage may remain the same for long periods of time or they may change with respect to time (= phyletic evolution). In any case, whether the phyletic lineage remains single or splits or whether it remains unchanged or modifies through time, no species limits exist between any temporal segments of a phyletic lineage. No matter how much phyletic evolution occurs in a phyletic lineage and no matter how different ancestral and descendent populations may appear, no species boundaries will be crossed as one traces a phyletic lineage; hence, transspecific evolution has not occurred.

A cross-section of a phyletic lineage at any point in time is a species. However, cross-sections of the same phyletic lineage at different points in time are not different species nor are they the same species. These are simply different cross-sections of the same phyletic lineage at different times; one would be ancestral to the chronologically later one.

The phyletic lineage is what is usually implied when the term phyletic species is used. I advocate the former term because it avoids confusion with the concept of species and because the relationship between the phyletic lineage and the species is clear.

Because the biological species concept is a non-dimensional one, it is not possible to speak of the age of a species, or of the origin of a species, or of the life and death of a species. It is meaningless to speak of evolution within the limits of a species and to contrast this mode of evolution with transspecific evolution or with evolution beyond the bounds of a species.

MECHANISMS OF EVOLUTIONARY CHANGE

It is possible to speak of many different types of evolutionary change and to formulate many mechanisms of evolution. These certainly exist and must be detailed if we are to comprehend the full scope of evolutionary biology. Yet it is possible to summarize all evolutionary change into two major types and to correlate these with the concepts of the phyletic lineage and of the species just discussed.

Phyletic Evolution

Phyletic evolution is change in a phyletic lineage with respect to time (Fig. 2). No mention should be made of a minimum time limit because this would become arbitrary. Thus phyletic evolution could be the change seen from one generation to the next. Only modifications that occur in an individual during its lifetime should be excluded from evolutionary change. Phyletic evolution does not have to be specified as hereditary change because this would preclude labeling many modifications (for example, those observed in the fossil record) as evolutionary because it would not be possible to demonstrate that they are hereditary.

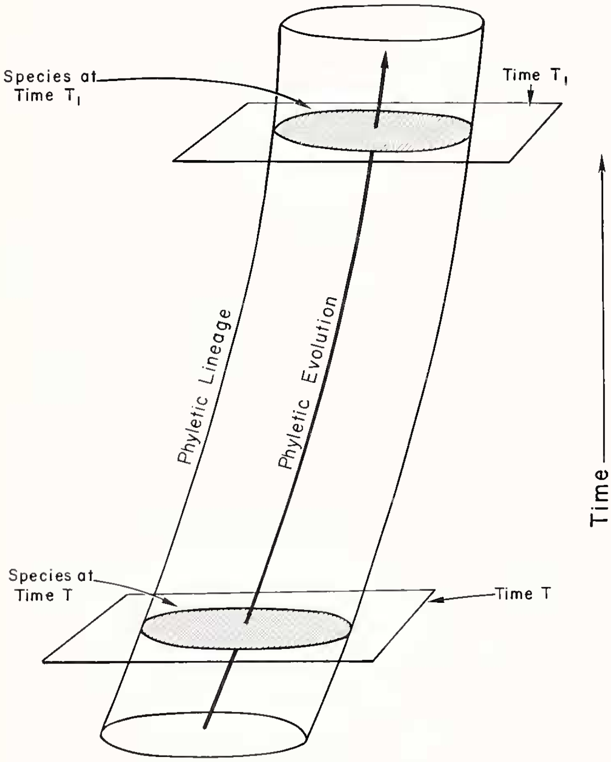


Fig. 2.—Schematic diagram to illustrate the concept of a phyletic lineage, which is a species reproducing itself generation after generation through time. Change in the species with respect to time is phyletic evolution. A cross-section through the phyletic lineage at any point in time is a species. Cross-sections at different points in time are neither the same species nor different species (no species boundary separates them) but simply different cross-sections of the same phyletic lineage.

In phyletic evolution, a descendent cross-section of a phyletic lineage would differ from an ancestral cross-section. Phyletic evolution can occur without speciation (splitting of the phyletic lineage) and, at least in theory, it would be possible to have drastic modification in the characteristics of members of a phyletic lineage by phyletic evolution without any speciation.

The mechanisms by which phyletic evolution occur can be summarized into two types—namely: a) the formation of genetically based phenotypic variation generation by generation; and, b) the action of natural selection arising from the interaction between the individual organisms and their external environment.

The formation of genetically based phenotypic variations is the accidental or chance based factor in phyletic evolution (Mayr, 1962). This genetically based individual variation in a population results from a number of mechanisms of which genetical recombination of all types (crossing-over, inversion, translocation, segregation) is the most important. These are the mechanisms which produce genetic combinations from the existing genetic material in the gene pool. Gene flow is the next most important mechanism, but far less important than recombination. It results in new genetic material in the population, but not new genetic material in the species. Mutations are the least important source for the production of generation by generation genetic variation; it is the source of new genetic material in the phyletic lineage.

Natural selection is the design factor in evolution and results from the interaction of individual organisms with their external environment. I am here concerned with the *mechanism* of natural selection not with its *result* of changes in gene frequencies in the gene pool (the usual definition of natural selection in population genetics). Selection can only result from the action of the external environment on the individual. It cannot arise from the "internal environment" or from the "genetic environment" nor can one speak about a distinct and separate form of "internal selection." Natural selection acts only on the phenotypes of individual organisms and

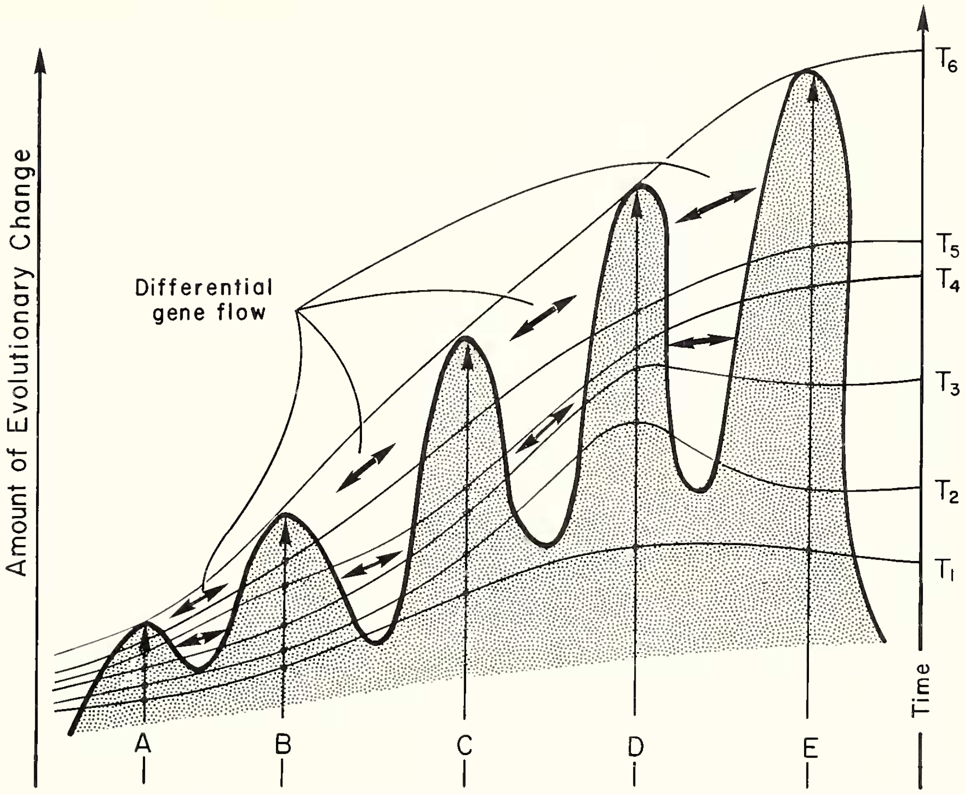


Fig. 3.—Schematic diagram to illustrate that populations of the same species can undergo different amounts of phyletic evolution (indicated by the differential points on the vertical arrows) during the same time period.

can distinguish only between varying phenotypes. The concept of selection is closely associated with that of adaptation (see below).

Both mechanisms of the production of genetically based phenotypic variation and of natural selection are required to have phyletic evolution. Both operate generation by generation and only in the present. Evolutionary change is the result of a chronological summation of the generation by generation simultaneous action of these mechanisms, not an average over a long period. Both mechanisms must be considered simultaneously as the creative mechanism of evolution, neither one or the other is sufficient by itself.

The rate of phyletic evolutionary change depends upon the combined action of these two factors. Rapid evolution cannot occur by mechanisms producing genetically based phenotypic variation alone or by strong directional selection by itself. Of special interest in explanation of macroevolution is the source of the needed directional selection.

It is possible to have varying rates of phyletic evolution in different populations of the same species (Fig. 3). The result will be variation in the amount of evolution in the sublineages of the same phyletic lineage.

Speciation

Speciation is the multiplication of species or the splitting of an original phyletic lineage into two or more lineages (Fig. 4). Speciation can only occur with the accompanying phyletic evolution in, at least, one of the two separated phyletic lineages. The essential aspect of speciation is the mechanism whereby intrinsic isolating mechanisms evolve in the two newly split lineages at a time when members of the two lineages would still be able to interbreed with one another.

Speciation, as I will use it, is only the multiplication of species. It is not phyletic speciation, which is a misnomer for phyletic evolution.

One of the major sources of confusion is: What is the fundamental aspect of the mechanism of speciation? Most workers are not clear about this and have confused many aspects of phyletic evolution in the notion of speciation. Is it the evolution of

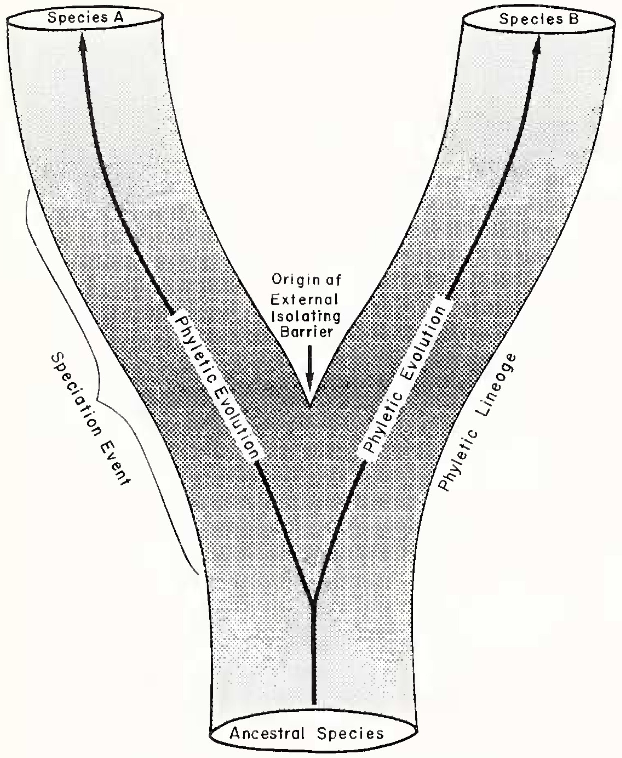


Fig. 4.—Schematic diagram to illustrate the relationship between speciation (splitting of a phyletic lineage into two lineages) and phyletic evolution. Speciation requires the presence of an external isolating barrier and of phyletic evolution in at least one lineage. Species A and B are distinct and separate from one another, but each is not different from the ancestral species common to both phyletic lineages.

intrinsic isolating mechanism? Is it the evolution of ecological, behavioral, and other differences between species that permit them to coexist? Is it the evolution of genetic differences that distinguish species? Moreover, most workers are not clear about the onset and about the completion of the speciation mechanism. Is speciation over when the two newly evolved species become sympatric without gene flow between them? Or does speciation continue for some time after the new species become sympatric?

I will accept the view that the essential characteristic of speciation is the evolution of intrinsic isolating mechanisms and of the ecological, behavioral, and other differences that permit the newly evolved species to coexist ecologically and without interbreeding. Clearly, speciation involves phyletic evolution, but I do not regard phyletic evolution as synonymous with speciation. Moreover, it is clear that the pattern and rate of phyletic evolution may differ in a small peripheral isolate as compared to a large central population or in a small isolate formed by a few founder individuals as compared to one formed by remnants left by a contracting species (Mayr, 1954), but these factors are aspects of phyletic evolution contributing to speciation, not speciation itself. Failure to separate these evolutionary mechanisms and to specify exactly what is meant by speciation has led to much confusion in macroevolutionary explanation.

The onset of speciation frequently occurs prior to the appearance of the external ecogeographical barrier and continues long after this barrier disappears and the two species are able to reinvade each others' range and coexist sympatrically (Fig. 5). Thus, I will separate speciation into two portions—the allopatric period and the neosympatric period.

Populations of a species may start to diverge before the appearance of an external barrier that splits the phyletic lineage into two separate sublineages. Hence at the onset of the allopatric phase of speciation the two sublineages may or may not be different from one another. The ecogeographical barrier (I will consider only allopatric or geographic speciation) splits the original single phyletic lineage into two and prevents members of the two sublineages from interbreeding during a period in which they could do so. The geographical barrier prevents gene flow between the two populations representing the split phyletic lineages. During the allopatric phase, the two populations will undergo separate phyletic evolution and will start to diverge from one another because each lineage is under the control of a different pattern of formation of genetically based phenotypical variation and of natural selection (Fig. 6). The rate of change in each population will depend upon a number of factors, including the size of the population, whether it was founded by a few individuals, and the nature of the environment and hence selection. Intrinsic isolating mechanisms may evolve during this period. If so, these isolating mechanisms appear fortuitously, both in their nature and time of appearance, as a pleiotrophic consequence of other evolutionary changes. Evolution of intrinsic isolating mechanisms is not under the control of selection favoring the evolution of isolating mechanisms.

During the allopatric phase of speciation, a certain and quite variable amount of divergence occurs between the two lineages. Generally, the amount of evolutionary divergence that occurs during this period is a minor amount of the total divergence between two sympatric and fully evolved species.

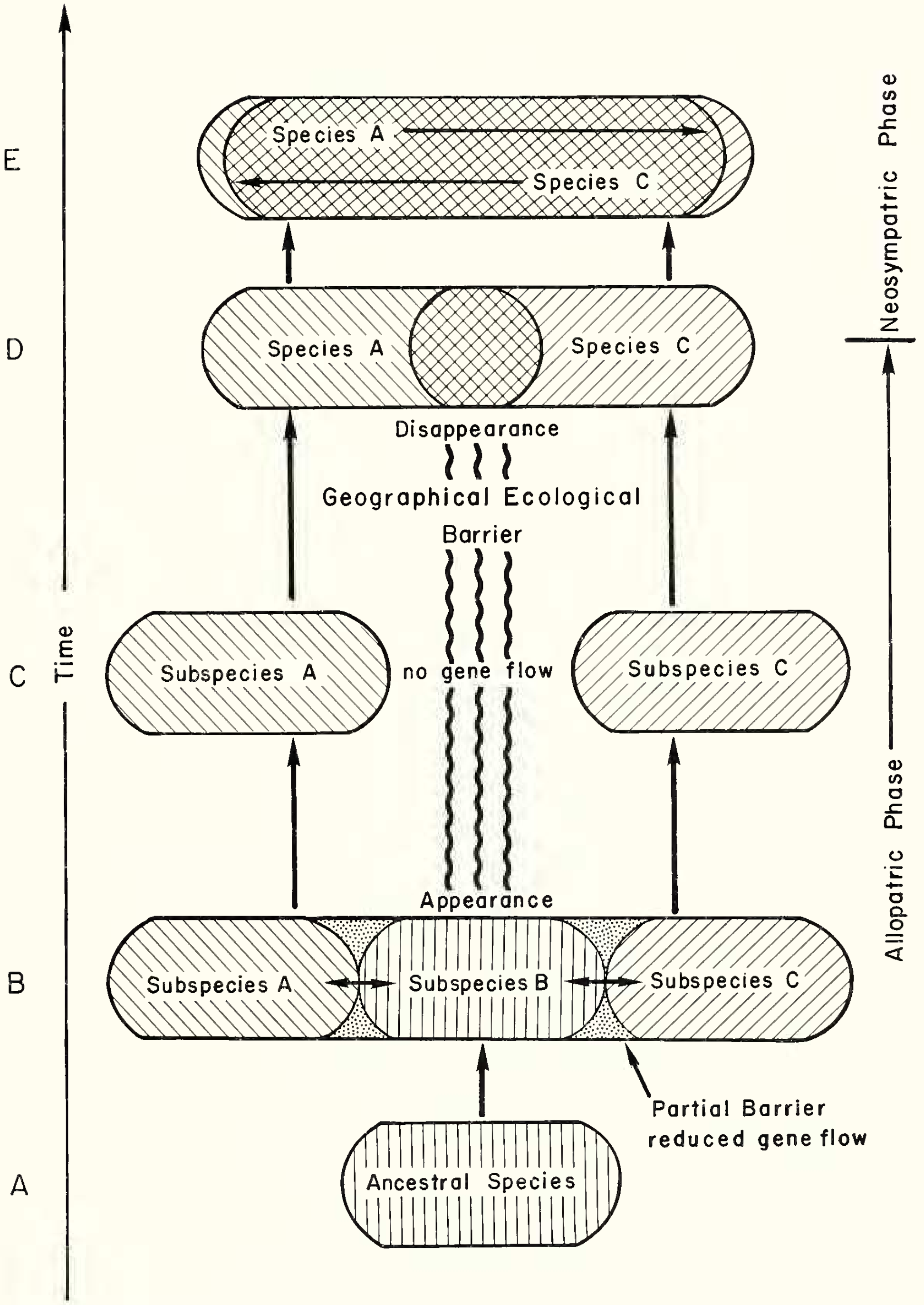


Fig. 5.—Schematic diagram to show the relationships of populations during speciation. The ancestral population (A) may have a period of subspeciation (B) before the appearance of a geographical-ecological barrier that separates two populations (C); this is the start of the allopatric phase of speciation. At this time no gene flow exists between the isolated populations (A and C). After the external barrier disappears, the two species are able to reinvade the geographic range of each other and to coexist if intrinsic isolating mechanisms exist (D); this is the start of the neosympatric phase of speciation. If sufficient ecological differences evolve between the species, geographic overlap can continue until the two species are broadly sympatric (E).

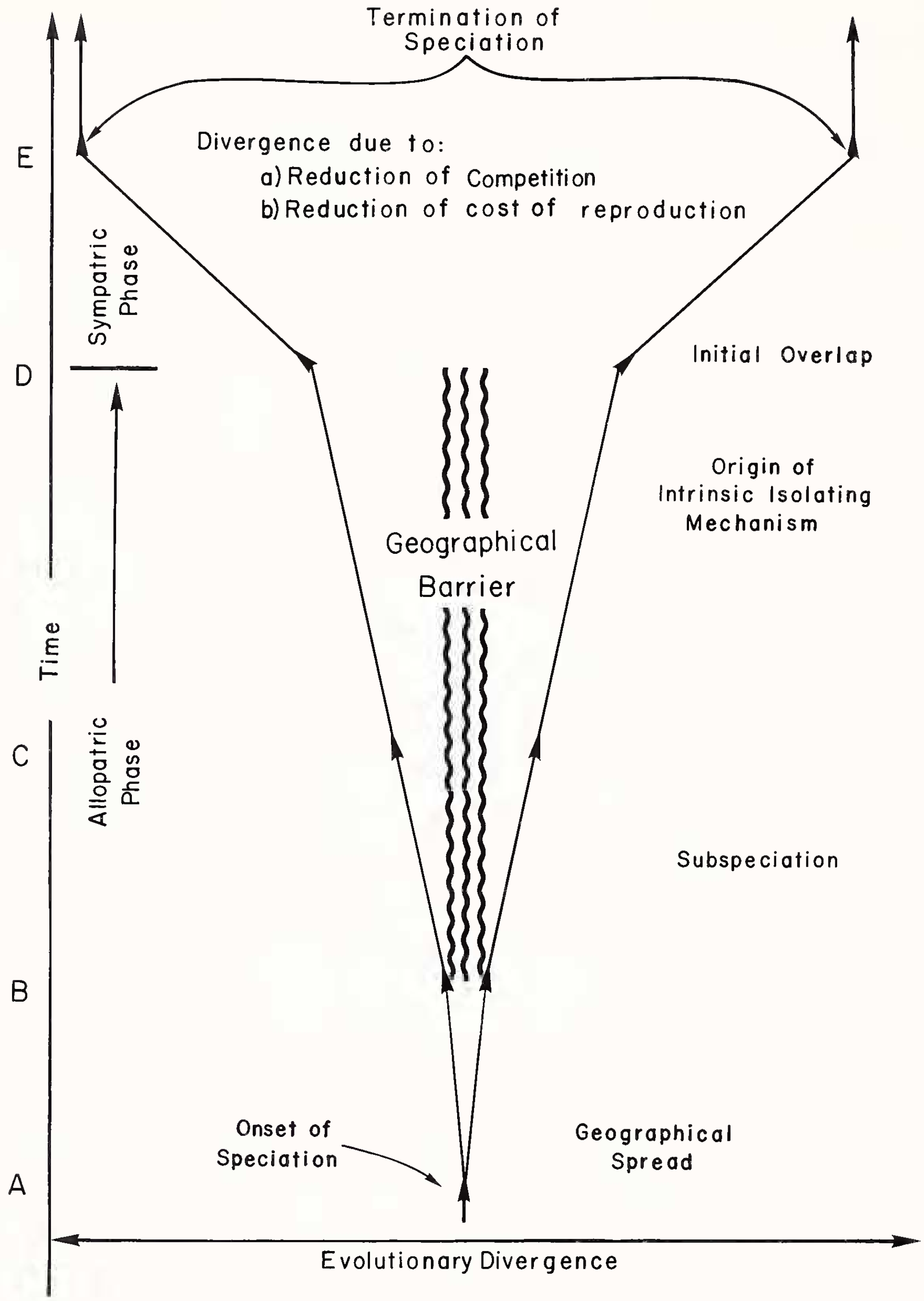


Fig. 6.—Schematic diagram to show divergence of the two phyletic lineages during speciation. The stages indicated by letters along the left edge correspond to those in Fig. 5. Rates of evolutionary change and resulting divergence are low during the period of subspeciation and somewhat higher during the allopatric phase after the appearance of the geographical ecological barrier. The rate of divergence increases sharply after the geographic barrier disappears and the two species become sympatric. Selection forcing the divergence during the sympatric phase arises from exclusionary species interactions between the two species. Speciation comes to an end when this period of rapid divergence terminates.

When the geographical barrier disappears, the two populations can expand their range and become sympatric as species if two conditions are met. The first is that the intrinsic isolating mechanisms evolved during the allopatric phase are 100% effective. This means that there is no gene flow between the two forms even if there is some hybridization. The second is that the two forms are sufficiently different ecologically that they are able to coexist. They need not be completely different or even largely different ecologically. All that is essential is that they differ somewhat so that each can invade the range of the other.

At the time of the breakdown of the external geographic barrier and the establishment of the initial overlap between the two species, the allopatric period ends and the sympatric or neosympatric period begins. This is not the end of the speciation process although most evolutionary biologists end their discussion at this point. For example, Mayr (1963) has almost no discussion of the events during the neosympatric period of speciation, which leaves a major gap between the genetics and ecology of speciation and the role of the species in transspecific evolution in his treatment of species and their evolution.

After the two newly evolved species become sympatric, they are able to interact with one another and thereby exert strong mutual selection on one another. The exclusionary species interaction (Bock, 1972) of the now sympatric species are of two types, namely (a) ecological competition, and (b) reproductive interference. The first type of interaction results from the fact that newly evolved sister species are frequently similar ecologically and still share many parts of their environment (see Lack, 1944, 1947, and elsewhere). The resulting competition will result in mutual selection on both species, which generally results in divergence of the feeding and other structures associated with the ecological competition. The second type of interaction results from the nature of the intrinsic isolating mechanism. When the two species overlap geographically, they must have 100% efficient intrinsic isolating mechanisms or else gene flow will commence between the two forms, which will lead to a breakdown of the distinctiveness of the two species. (I reject the notion that the isolating mechanisms can be less than 100% effective and that selection during the neosympatric period can improve these isolating mechanisms from less than 100% to 100% effective.) Yet intrinsic isolating mechanisms can be 100% effective and vary greatly in their reproductive cost. By reproduction cost, I mean the percentage of a particular breeding period that an individual wastes because it attempts to breed with a member of another species. Such a wastage of time will reduce the number of offspring that individual could have. If one examines the classification of isolating mechanisms presented by Mayr (1963:92), these mechanisms are arranged from high reproductive cost at the bottom of the list (F_1 hybrid zygote fully viable, but sterile) to low reproductive cost at the top (seasonal, habitat, and ethological isolation). Selection will favor isolating mechanisms of lower reproductive cost; hence during the neosympatric period selection arising from species interaction would select for new isolating mechanisms of lower reproductive cost than those existing at the time of initial sympatry. Although this selection is for isolating mechanisms, it is not to improve the efficiency of the isolating mechanism but to reduce reproductive cost. Evolution is from an isolating mechanism that is 100% effective but has high reproductive cost to one that is 100% effective but has low reproductive cost. There has been no improvement in the isolating mechanism, but in reproductive cost. This selection will favor the evolution of courtship displays, more elaborate species-specific recognition characters (color, horns, plumes, song, and others) and temporal separation of breeding seasons.

Features acted upon by the mutual selection from the two species under exclusionary species interaction will diverge rapidly and considerably. These are often features associated with feeding (ecological competition) and with species specific recognition (reproductive cost). They are generally those features which distinguish sympatric species most readily especially in contrast to allopatric, closely related species. Selection arising from these exclusionary interactions are frequently the strongest known natural selection and presumably cause the most rapid evolutionary change. I have postulated (Bock, 1972) that most of the divergence between sister species results from the mutual selection arising from exclusionary species interaction during the neosympatric period of speciation. This is after the two sister species are able to reinvade each other's range after the breakdown of the geographic barrier and after the perfection of the intrinsic isolating mechanism (100% effective). This assertion is in direct variance with that made in some quantum theories (for example, rectilinear model of macroevolution) which assumes that the major change occurs prior to the breakdown of the external barrier and the onset of sympatry of the sister species. It can be tested by comparing the amount of divergence observed between allopatric sister species and fully sympatric sister species in closely related taxa (that is, members of the same genus or closely related genera). A rough survey of such species in birds supports the hypothesis that most evolutionary divergence between sister species takes place during the sympatric portion of speciation.

Speciation would be terminated when the exclusionary species interaction and the resultant mutual selection force between the sister species approaches the zero level. Quite possibly one or both of the phyletic lineages of these sister species could have split again and entered a new cycle of speciation before the termination of the original cycle.

Speciation and Macroevolution

Macroevolution is simply a large amount of phyletic evolutionary change. It is a summation of a number of microevolutionary phyletic events, often in a relatively short time. Speciation, per se, has nothing to do with major evolutionary change if one regards speciation as the mechanisms permitting the multiplication of species—evolution of intrinsic isolating mechanisms. Yet the phenomenon of speciation, especially repeated speciations, is an important factor in macroevolution because the selection forces arising from species interactions during the neosympatric phase of speciation is an important driving force in macroevolution (Bock, 1970, 1972). Thus the relationship between speciation and macroevolution or the role of the species in macroevolution is that a major driving force for macroevolutionary evolution comes from the selection forces arising from the exclusionary species interactions between sister species during the neosympatric phase of speciation (as well as between other sympatric species). Another important driving force is coevolutionary interactions for which repeated speciations are less important. Thus, the more speciations (repeated cycles of speciation) and the more species which interact, both exclusionary and coevolutionary, the stronger and the longer in time will be the driving directional selection force required for the phyletic evolution that will result in a major evolutionary change.

Although this assertion may sound like that of punctuated equilibria or rectilinear evolution, it is very different. In the punctuated equilibria model, macroevolution is regarded to be the consequence of a repeated series of speciations. That speciation is *the* essential evolutionary mechanism. Phyletic evolution, which is synonymized with phyletic gradualism, is regarded to be insignificant to the point of being nonexistent. In the punctuated equilibria model, most of the change is assumed to occur during the allopatric period of speciation. In the synthetic model advocated here, most of the change is postulated to occur during the neosympatric period (plus the change resulting from coevolutionary interaction which occurs continuously).

Unity of the Genotype

At this point a digression must be followed to consider the concept of the genotype and of the gene pool of the species as discussed by Mayr (1963:263–296, and elsewhere). Closely associated with this concept is that of genetic revolution (Mayr, 1954, 1959, 1963). The basic concept is the cohesion of the genotype of the individual and of the gene pool of the species. The adaptive value of individual genes is not an absolute intrinsic property of each gene, but is dependent upon "coadaptive" interaction between the gene and the remainder of the genotype. The adaptive value of the gene varies according to the genotype. Cohesion of the gene pool of a population or the interbreeding populations of a species is dependent upon the multiple patterns of gene flow throughout the species (Mayr, 1954, 1959, 1963). It is the phenomenon of gene flow that is the critical factor. It should be noted that many recent evolutionists reject gene flow as an important evolutionary factor, including some workers who accept fully Mayr's concept of genetic revolution.

Mayr argues that elimination of gene flow resulting from isolation of a population will have a great effect on the consequence of selection on that population because the genes affected by selection are acting against a different genetical background and will have a different adaptive value. The effect of the disruptive effect of isolation will be greatest for a new population established by a few founder individuals. It would be next greatest for a small isolate resulting from the appearance of a barrier that cut it off from the remainder of the species. This frequently happens when the range of the species shrinks leaving isolates in pockets of favorable habitat. The effect is smallest for a species with a large range that was divided into two subequal segments. In such examples, divergence would be slowest, but it would still occur as shown by the many examples of eastern and western species or well-marked subspecies of North American forest birds (for example, *Colaptes, Contopus, Cyanocitta, Dendroica, Oporornis, Icterus, Pheucticus, Passerina*—Mayr and Short, 1970).

Mayr stresses the importance of selection acting on the genetical modification resulting from the disruption of the gene flow. He argues that the consequence of selection acting on genes whose adaptive value has been altered because of the changed genetical background may result in a major change which he termed a genetical revolution. Such alteration in adaptive value of genes would be greatest in populations originating from a few founders. Carson's (1975) model has similar elements in that he includes a population crash that results in a few founder individuals from which the subsequent populations originate. In Mayr's model the founders are considered as individuals that have invaded a new area. Problems exist with the concept of genetic revolution because other workers have deemphasized the importance of selection and have argued that speciation must be associated with a genetical modification without the action of selection. The general notion is that this genetical revolution has occurred completely during the allopatric phase of speciation prior to the reestablishment of sympatry. This implies that evolutionary change as expressed in the phenotype would have occurred prior to the reestablishment of sympatry of the sister species.

The concept of the unity of the genotype and of the gene pool, the concept of variable adaptive value of genes depending upon the genotypic background, and the concept of genetic revolution are all sound and are supported by a considerable mass of observations. However, a number of aspects of genetic revolution and its bearing on macroevolution have not been discussed by Mayr or by other workers who have accepted these ideas in their development of quantum theories.

One of the most important is what are the types of phenotypic features that are usually affected by genetical revolutions. Are these parts of the feeding apparatus, the locomotory system, or external features which may be associated with species-specific recognition characters? To be sure, many examples of distinctive subspecies or allopatric species exist whose evolution is well explained by the concept of genetic revolution. But the features that have been modified are usually not features characteristic of major evolutionary change. What is needed at this point are surveys of the features affected by genetic revolutions, not only of taxa that support this concept.

The second problem is that Mayr quite rightly argues that his concept of genetical revolution places emphasis on the essential and central role of natural selection which is too often ignored. Mayr points out that the genetically based phenotypic variation in the founder population available for selection differs greatly from that in the main population because of the disruption of gene flow. What is not discussed is the source of this selection and the time at which this selection acts. Clearly, in many examples, this selection has acted during the allopatric period of speciation because the taxa being compared are still allopatric. But, one must examine the features modified and consider the possible environmental source of the selection. Disruption of gene flow and evolutionary change during the allopatric period may provide the needed genetically based phenotypic variation for the change during the sympatric phase. Selection may arise largely from species interactions, both exclusionary (from forms other than the sister species) and coevolutionary, during the allopatric period as noted by Mayr (1954) who points out that particularly the biotic environment of an isolate may differ from the rest of the species. Nothing in the concepts of disruption of gene flow and of genetical revolution as advocated by Mayr would conflict with the concept that the major selection forces arise from species interactions and that most of this selection acts during the sympatric phase of speciation after the intrinsic isolating mechanisms are completely effective.

COMPARISON

Most of the testing of models of macroevolutionary explanation is by comparison and interpretation of characteristics of different forms. Moreover, one of the important conceptual steps in the synthetic model is dependent upon proper interpretation of comparison and the extrapolation from one type of comparison to another. This conceptual step is not limited to the synthetic model, but exists in all ex-

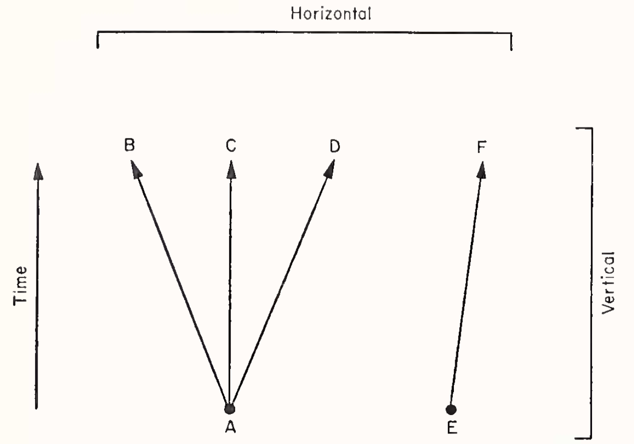


Fig. 7.—Schematic diagram to show the difference between horizontal comparisons and vertical comparisons. Vertical comparisons are those between members of the same phyletic lineage, for example, between A and B, or A and C, or A and D, or E and F, along the time axis. Horizontal comparisons are those between members of different phyletic lineages, for example, between members of lineages A–B, A–C, A–D, and E–F, no matter if the forms being compared are or are not at the same time level (taken from Bock, 1967:Fig. 1).

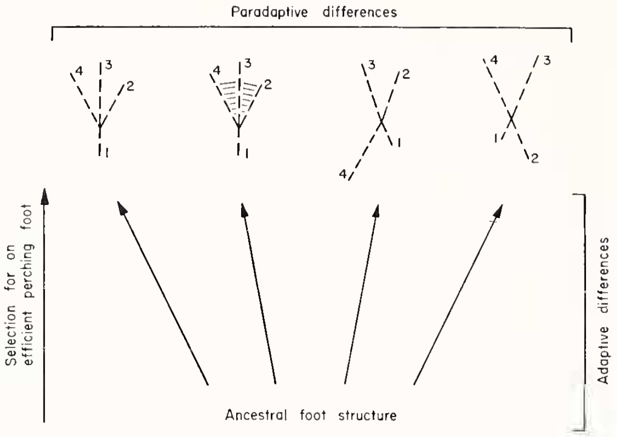


Fig. 8.—Schematic diagram to show the pattern of multiple pathways of evolution of perching feet in birds. Evolution of the four different arrangements of the toes from the ancestral configuration was under the control of the same selection force for a more efficient perching foot. Differences observed in vertical comparisons are adaptive, whereas horizontal differences are paradaptive with respect to the selection force controlling the evolution of these adaptations (taken from Bock, 1967:Fig. 2).

planatory models of macroevolution. Little discussion exists on principles of biological comparison, especially on the theoretical level; I will refer mainly to comments in my earlier papers (Bock, 1967, 1969, 1977).

Not all comparisons in biology are the same and the interpretations reached on the basis of a particular comparison cannot be extrapolated simply to all others. Not all comparisons are between members of different species, excluding the case of comparison between conspecific individuals. Although comparisons can be made for many diverse purposes and with many goals in mind, they can be divided into two major categories—horizontal and vertical (Fig. 7). This dichotomy does not exhaust the possible classifications of types of comparison; it is one that is of particular relevance to the development of macroevolutionary theories.

Horizontal comparisons are those across phyletic lineages—between members of different phyletic lineages and hence, between members of different species. They can be between species at the same point in time or at different points in time so long as they are between different phyletic lineages. Comparisons between conspecific individuals at the same time period would be horizontal.

Vertical comparisons are those within a phyletic lineage—between members of the same phyletic lineage at different points in time. These are comparisons between ancestral and descendent cross-sections of the same phyletic lineage and hence, are not between different species.

It is not possible to extrapolate simply from horizontal comparisons to vertical comparisons. Horizontal similarities are not the same as vertical similarities and horizontal differences are not equal to vertical differences. The origins of these two types of similarities and of these two types of differences may be quite different and hence will require diverse explanations. For example, differences observed in a horizontal classification may have nothing to do with adaptation and are designated as paradaptive (Bock, 1967; and see below) yet the vertical difference in each phyletic lineage may be adaptive. The conclusion offered earlier that the evolution of features is not adaptive if their horizontal differences are not adaptive is simply in error.

The difficulties in extrapolating interpretations from a horizontal to a vertical comparison and vice versa is the consequence of the simultaneous action of two evolutionary mechanisms in phyletic evolution. These are, of course, the production of genetically based phenotypic variation, which is chance-based, and the action of natural selection, which is a design mechanism. These mechanisms act in the phyletic evolution of every lineage. Hence, given the existence of a particular selection force acting on a species, it is not possible to predict the future course of phyletic evolution and the resulting adaptation, if any, because it is not possible to predict the outcome of the chance-based genetical mechanisms.

The concept of multiple pathways of evolution (or adaption) stems directly from the action of these two evolutionary mechanisms and their consequences as interpreted in horizontal and vertical comparisons (Bock, 1959; Bock and deW. Miller, 1959). Different adaptive answers (Fig. 8) may appear and evolve in several lineages under the control of the same selection force as shown by the evolution of different perching foot types in birds (Bock and deW. Miller, 1959). Associated with this idea is the concept of paradaptation (Bock, 1967). Paradaptive differences are ones between different multiple adaptive answers and are the consequence of the chance-based genetical mechanisms (Fig. 8).

The conceptual step, which will be necessary in the development of the synthetic explanation of macroevolution, is to formulate a (pseudo)phylogeny of steps leading to a major change using horizontal comparisons of closely related forms (for example, congeneric species) and to interpret the differences as adaptive steps. Then this horizontal sequence must be transposed to a vertical sequence which is the key conceptual step. This is one that is difficult to support by empirical observations as one requires known phylogenies (that is, those of domesticated animals and plants). Moreover, it is a conceptual step that falls in the realm of a link or bridge between theories. A worker is free to reject or accept it. However, if rejected, then much of the basis for developing and testing explanatory models, both quantum and synthetic, of macroevolutionary change is eliminated.

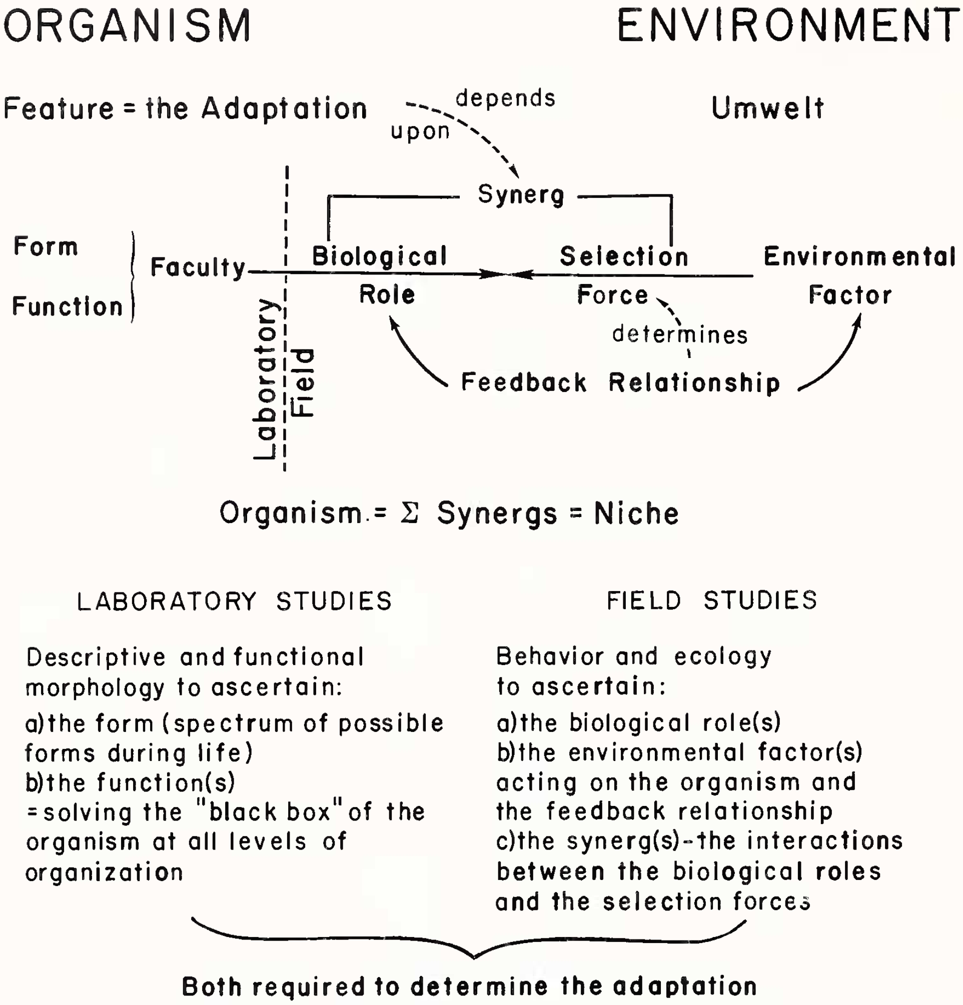
In developing the synthetic model and in discussing supporting examples, I will give particular attention to this conceptual jump between horizontal and vertical comparisons.

ADAPTATION

The key to all explanatory models of macroevolution is the concept of biological adaptation. What is an adaptation and how are individual adaptations ascertained? How do adaptive features evolve? What is meant by adaptive evolution of features and by adaptive evolution of a population under the overall notion of adaptive phyletic evolution? Is the adaptive evolution involved in the origin of a new major feature or of a new major taxon (adaptive radiation) different qualitatively from adaptive evolution on the microlevel?

The concept of biological adaptation has always been used to designate features of an organism, which operate well in the particular environment of that organism. Hence wings of most birds are adaptations for aerial flight, whereas the wings of penguins are adaptations for underwater flight. The concept of adaptation long predates ideas of biological evolution and indeed the attempt to provide a scientific explanation for adaptation led to the formulation by Darwin of the concept of organic evolution by natural selection. An adaptation is a feature of the organism. Individual features or complexes of features are adapted to particular components of the organism's environment. It is almost of no interest to inquire whether a whole organism is adapted to its environment—it must be, otherwise it would be dead. The questions of interest are what is the adaptive significance of individual features and how each adapted feature contributes to the survival or to the fitness of the organism.

An adaptation is, thus, a feature of the organism, which interacts operationally with some factor of its environment so that the individual survives and reproduces. Stress is placed on the organism surviving as an individual because it cannot otherwise reproduce. However, adaptations cannot be judged only with respect to survival of the individual; it must survive and reproduce. Adaptations must be judged with respect to a particular environment and always on a probability basis with respect to present (and possibly past) environmental conditions, but never against future factors. The environment is the external environment, be it biotic or physical. Hence the concept of adaptation is defined and individual adaptations are judged with respect to selection forces arising from the external environment and acting on the organism. Adaptation does not designate operational relationships between parts of the organism or an operational relationship of a feature to the "internal environment." Notions such as "the internal environment," or "the genetical environment," or "internal selection" are misleading to the extreme and should be abandoned. Mus-



LABORATORY STUDIES

Descriptive and functional morphology to ascertain:
a) the form (spectrum of possible forms during life)
b) the function(s)
= solving the "black box" of the organism at all levels of organization

FIELD STUDIES

Behavior and ecology to ascertain:
a) the biological role(s)
b) the environmental factor(s) acting on the organism and the feedback relationship
c) the synerg(s)–the interactions between the biological roles and the selection forces

Both required to determine the adaptation

Fig. 9.—Simplified scheme illustrating the laboratory and field studies required for the direct analytic determination of an adaptation. The adaptation is the feature and is reflected in the details of its form-function complex or faculty. The existence of an adaptation is dependent on the existence of a synergical interaction between a biological role of the feature and a selection force. No synerg means no adaptation. A feature may represent a single adaptation or a number of adaptations depending on the number of synergical relationships between the feature and the umwelt of the organism. In the latter case, the form of the feature and hence its functions (that is, the properties of the adaptation) may represent a compromise between conflicting selection forces. Additional investigation is needed to measure the degree or the goodness of the adaptation (taken from Bock, 1978:Fig. 1).

cles are not adapted to bones, but these anatomical systems are integrated ones that are adapted to selective forces arising from the external environment. A clear distinction must be made between the concept of mutual adjustment of features, which is critical to the adaptiveness of features, and the vague notions of adaptation to internal or genetical environments.

The concept of adaptation is not the same as survival of the species (especially over a longer period of time) or the same as fitness. These are different evolutionary concepts; the synonymy of adaptation to either one or both of these other ideas has lead to great confusion in the elucidation of these evolutionary concepts. Rather the concept of adaptation is related to these other concepts in that the adaptiveness of features contributes to the fitness of individuals and to the survival of the species. What is needed are more accurate measures of adaptation so that the contribution of individual adaptations to fitness or to survival can be judged more precisely.

Adaptations, being features, are parts of the phenotype of the individual. Genes, per se, are not adaptations. Genes can be said to be adaptive or to have adaptive value if they contribute to the ontogenetic development of an adaptive feature.

Each adaptation must be determined individually by direct analysis; the comparative approach is invalid for determining adaptations (Bock, 1977). Comparisons can be made only after the individual adaptations had been established. Recognition of adaptations depends upon careful separation and delimitation of properties of features and of the relationships between the environment and the organism. I will rely upon the set of ideas advocated earlier by von Wahlert and myself under the heading of "Adaptation and the form-function complex" (Bock and von Wahlert, 1965). The relationships between these concepts are illustrated in Fig. 9.

Feature

The adaptation is a part, trait or feature of the organism; the feature can be defined (Bock and von Wahlert, 1965:271) as: *a feature is any part or attribute of an organism if it stands as the subject in a sentence descriptive of that organism.* Thus a feature can be any part of the organism, its delimitation depending only upon the interests of the investigator. A feature can be any attribute of the organism, be it a behavioral, physiological, or biochemical trait; it need not automatically be an anatomical structure. Moreover features can be taken from any level of organization within the organism, for example, a muscle cell, or a muscle, or a muscle-bone system, and so forth; the consequences of these levels of organization must always be recognized.

Form

The form of a feature is those properties of material composition, configuration, and appearance that are generally grouped together under the heading of its morphology. It may be defined formally (Bock and von Wahlert, p. 272) as: *in any sentence describing a feature of an organism, its form would be the class of predicates of material composition, and the arrangement, shape, configuration, and appearance of these materials at all necessary levels of organization; these predicates need not make any special reference to the normal environment of the organism.* It must be emphasized that a particular feature in an individual usually does not have a single form as commonly believed by morphologists. Most features modify over the life of the individual; some change irreversibly, some reversibly. Teeth wear and feathers become frayed. Or the shape of flight feathers alter according to the air pressure impinging upon them. The feature may modify slowly under the action of particular stimuli (the phenomenon of physiological adaptation, Bock and von Wahlert, 1965:284–285, which is synonymous with somatic change, Bateson, 1963), such as the change in bone structure under the influence of mechanical stresses. Or the feature may change its form quickly and reversibly as they are used. Muscles may undergo radical changes in their form during each contraction cycle, the lens of the vertebrate eye may undergo change in its curvature, the size of the stomach modifies during the course of a large meal; these possible modifications in form must always be noted. Thus, one cannot assume that a feature has a single form as shown by the specimen lying on the dissection table, but that it possess a spectrum of form, which may change by wear or other environmental forces, or slowly by physiological adaptation, or rapidly by physiological action, or any combination of these mechanisms.

Function

The concept of function is a most controversial one and the following definition is not accepted by many biologists. Most problems arise because the term function is used for at least two quite separate and distinct concepts—that of function (as used herein) and that of biological role. It is not possible to discuss the concept of biological adaptations meaningfully unless these two concepts are carefully distinguished regardless of the names used to designate them. Unfortunately most workers continue to confuse and interchange these concepts by using function as a single broad term covering both. It is essential to separate the concepts of function and of biological role, and to use the terms consistently; I advocate, but do not insist on the concepts and terms as defined below. However, I do insist on a separate and consistent usage whatever terms are used.

Basically the function of a feature is its action or how it works. It is that aspect of a feature studied by physiologists and functional morphologists. It may be defined formally (Bock and von Wahlert, 1965:274) as: *in any sentence describing a feature of an organism, its functions would be that class of predicates which include all physical and chemical properties arising from its form (that is, material composition and arrangement thereof), including all properties arising from increased levels of or-*

ganization; these predicates need not make any special reference to the normal environment of the organism. The properties of function are, in this definition, absolutely bound to the properties of form via chemical and physical laws. A feature will have numerous functions, which may include many never used by that organism. Functions may be classified into utilized and nonutilized ones depending upon whether they are associated with biological roles of that feature.

Although this definition of function may appear awkward to many evolutionary biologists, it has many advantages in addition to being nonambiguous. It is close to the idea of function used by many or most physiologists, biochemists, and other "functional biologists." It frees the concept of function from all associations with teleology or teleonomy (Bock and von Wahlert, 1965:274). It forces the biologist to consider all possible functions of a feature, often revealing several unsuspected ones. And it provides a clearer understanding of some evolutionary concepts such as preadaptation (that is, the source of the "new functions" at this period of "functional change") and such as the correlation between change in form and in function during evolution (that is, they must change hand in hand—it is the biological role via the behavior that generally changes before the form of the feature).

It must be emphasized that care must be exercised in the application of a number of evolutionary statements if the above definition of function is accepted. Most of the statements in the morphological and the evolutionary literature use "function" in a broader or vaguer sense, and hence the statements may no longer be correct with this narrower concept of function. Each of these evolutionary statements or principles must be checked to ascertain its validity with this more restrictive definition of function.

Faculty

The two classes of properties of a feature are its forms and its functions. It is valuable to have a term by which they can be discussed together—the form-function complex or the faculty—because it is this form-function complex of the feature, which determines its adaptive significance, not the form alone or the function alone. The form-function complex or faculty of the feature may be defined (Bock and von Wahlert, 1965:276) as: *a faculty is defined as the combination of the form and one of the functions of a feature.* An expanded definition can be formed by combining the above definitions of form and of function.

The feature will have as many faculties as combinations of the form and the several functions. If the form varies during the life of the organism, with the correlated change in functions, then the faculties will also vary. A feature may have faculties that are not used by the organism during its normal life; utilized faculties are those that have a biological role and interact with a selection force. The faculty is the unit acted upon by natural selection and is the aspect of the feature that is adapted to the environment. Because a feature usually has a number of faculties, which interact with different selection forces, the final adaptation—the final form and functions of the feature—is frequently a compromise.

Biological Role

The biological role is how the organism uses the faculty and hence the feature in the course of its life history; the use may be active or passive. The biological role may be defined (Bock and von Wahlert, 1965:278) as: *in any sentence describing a feature of an organism, its biological roles would be that class of predicates which include all actions or uses of the faculties (the form-function complexes) of the feature by the organism in the course of its life history; these predicates must make explicative reference to the normal environment of the organism.* Essential to the description of a biological role is observation of the organism living freely in its natural environment. A biological role cannot be determined by observations made in the laboratory or under other artificial conditions. Studies by functional morphologists, no matter how detailed or how carefully done, cannot elucidate biological roles so long as this work is done in the laboratory.

Functions can be ascertained from the form of a feature if one knows the causal relationships between the form and the function as dictated by the chemical and physical laws. Hence it is possible to ascertain the function of features by a comparison of the forms, that is, the function of a feature can be obtained from a knowledge of its form. The causal relationships between the faculty (or the form) of a feature and its biological roles is much looser so that it is usually not possible to ascertain the biological role of a feature by comparison or by a knowledge of the form. Hence determination of biological roles is especially difficult in fossils or in

Recent organisms whose life histories are not known.

Statements that the function of a feature cannot be ascertained from a knowledge of its form refer to the biological role, not function, according to the above definitions. Statements about "functionless features" refer to those features that do not possess any biological roles. It is possible, at least theoretically, for a feature to lack biological roles as in the case of a feature, which evolved as a pleiotrophic consequence of some other feature or in the case of a vestigial feature. However, it is not possible to have functionless features because the existence of a form of a feature automatically implies the existence of some functions under the definitions advocated herein.

The study of the biological role(s) of a feature is a definite behavioral-ecological analysis. The leg of a mammal may have locomotion among its several functions, with parameters of speed, rates of fatigue, and so forth, but its biological roles may vary from catching prey or escaping from a predator to migration or courtship display. Large mucus secreting salivary glands are found in a number of birds with a function of the mucus being that of a glue—to stick objects together. However, the biological roles vary from feeding by trapping insects on the tongue in woodpeckers, to nest construction in swifts and some swallows, and to food storage during winter months in the Gray Jays (*Perisoreus*).

Environment

The environment of an organism includes all physical factors and biotic factors impinging on it, the latter being various types of species interactions (Bock, 1972), which appear to provide the largest and the most severe part of the total selection on the organism (see also Darwin, 1859:487–488). All of the environmental factors, which could possibly be utilized by the organism, or, which could possibly act on that organism, comprise the umgebung; it is the sum of the environmental factors generally called the habitat. The umgebung may be recognized without the actual presence of the organism although some knowledge of the features and the life history of the organism is needed to judge the suitability of the habitat.

Those factors of the environment, which are actually being used by the organism, or, which are actually acting on it, comprise the umwelt or the species-specific habitat. The umwelt can be ascertained only in the presence of the organism living naturally in its environment. The umwelt is a subgroup of the environmental factors comprising the umgebung. The umwelt, being the species-specific habitat, changes as the species evolves (the causal relationships are reversed, however) and disappears when the species becomes extinct. Environmental factors are not, however, restricted to the umwelt of a single species. A water hole on the African veld may be used by a number of species. All tetrapods and many other organisms use atmospheric oxygen which is common to the umwelt of all these species.

The factors of the umwelt are designated as the niche by many biologists; I prefer to use this term for the total interaction between the organism and its umwelt (see below).

The definition of natural selection is difficult because a complete definition should include the mechanism by which the environment acts and the result of this environmental action (Bock and von Wahlert, 1965:291). Geneticists have stressed the latter in defining selection as the non-random differential reproduction of genotypes (a result definition). Without gainsaying the importance of this aspect in the definition of selection, I wish to concentrate on the mechanism because I am concerned with the causal interrelationships between the environment and the organism. Thus, the mechanism of natural selection is an interaction between the umwelt of the organism and the phenotype of that organism. The environment places demands on the organism with which it must cope if the organism is to continue to survive as an individual. An individual selection force is the action of a single environmental factor of the umwelt on the phenotype of the individual (that is, on a feature) through a particular biological role of a faculty of that feature. A selection force can act simultaneously on biological roles of several features. The nature of a selection force is not determined automatically by the umwelt factor, but depends upon the umwelt factor and how the organism reacts to that factor. A feedback relationship exists between the factor of the umwelt and the biological role of the faculty (von Wahlert, 1965; Bock and von Wahlert, 1965:282) which determines the final nature of the selection force. Because of the active contribution of the organism through a particular biological role and the factor of the umwelt in creating the exact selection force, this link is called a synerg to indicate the actual working together of the organism and the environment (see von Wahlert, 1973, and elsewhere).

The *synerg* may be defined (Bock and von Wahlert, 1965:281) as *the link between the organism and its umwelt formed by one selection force of an environmental factor of the umwelt and one biological role of a faculty.* Although this definition uses the selection force as the environmental side of this link, it must be remembered that the feedback mechanism of this interaction extends from the organism beyond the selection force to the environmental factor itself. Most selection forces and most biological roles participate in more than one interaction, and hence each may take part in the formation of a number of different synergs of the organism.

The synergs in which an organism partakes in its interaction with the umwelt must be maintained if the organism is to survive as an individual. The sum of all the synergs can be defined as the niche (Bock and von Wahlert, 1965:282). Thus the *niche* may be defined as *the total relationship between the whole organism and its complete umwelt.* The niche is the relationships between the organism and the umwelt—not the total environmental factors of the umwelt—and cannot be recognized without the presence of the organism. No organism means no niche. The niche changes as the species evolves and disappears if the species becomes extinct. Empty niches do not exist. The logical and useful extension of this concept is that the niche is the species. After all, a species is not just the object we can see and describe, but it is the total complex of interactions of this object with its umwelt. The niche, being the total of synergs, describes the total selection of the umwelt on the organism.

Changes in a selection force (or in the total selection) are associated with changes in the synerg (or the niche) and may be associated with modification in the environmental factors of the umwelt, but they need not be. It is possible to have modifications in synergs and hence the niche as the result of the organism reacting differently to the same factor of the umwelt and thus modifying the resulting selection (see von Wahlert, 1961, 1965, 1973; Bock and von Wahlert, 1965:282). Hence adaptations may evolve in response to new selection forces acting on the organisms, but these new selection forces do not have to be coupled with new or different environmental factors of the umwelt.

Adaptation

The concept of biological adaptation has always designated the phenomenon of the organism being well suited to (that is, able to cope with) the demands of its environment. Adaptation has been used in several senses (Bock and von Wahlert, 1965:282–285)—universal adaptation, physiological (= functional or somatic) adaptations, and evolutionary adaptation; I will be concerned only with the last. Evolutionary adaptation connotes both a state of being and a process, but the distinction between the two is usually clear. As a state of being, it makes sense only to speak of individual features of an organism as adaptations; to designate a whole organism or a population as an adaptation is without useful meaning.

Adaptation, both the state of being and the process, must always be stated with respect to a particular environmental factor of the umwelt. Moreover, the feature is not adapted to the environmental factor but to the selection force resulting from the feedback interaction between the organism and umwelt factor. Hence adaptation must be defined and must be judged with respect to definitely delimited selection forces. (Adaptations are often judged with respect to definitely delimited umwelt factors which is not quite correct, but is sufficiently accurate for most studies.)

An adaptation is a feature of an organism that has at least one biological role interacting with a selection force—it forms a synerg. *An adaptation, the state of being,* can be defined as *a feature having properties of form and function which permits the organism to maintain successfully the synerg between a biological role of that feature and a previously stated selection force.* Note that the selection force must be given prior to the statement of the adaptation. By successful, I mean that the individual organism survives as an individual and reproduces to leave progeny in the next generation. Adaptations must be judged on a probability basis and against present (and possibly past) environmental conditions, never against future factors. Success is a relative term and some measure of success or of the relative degree of goodness of the adaptation is needed. Bock and von Wahlert (1965:286–287) suggested that the degree of adaptation could be judged by a measure of the amount of energy required by the organism to maintain the synerg—a sort of efficiency judgment. This is not an optimizing concept of adaptation similar to that advocated by many evolutionary biologists and ecologists. Hence *the degree of adaptation, the state of being,* is defined as *the amount of energy required by the organism to maintain successfully* *the synerg of the stated adaptation with a lower energy requirement indicating a better degree of adaptation.* Thus the degree of adaptation is inversely related to the energy required to maintain the synerg. It must be noted that the degree of adaptation is judged for a stated adaptation and that the adaptations are determined relative to a stated selection force. Energy requirements must always be given in terms of calories—gm-wt^{-1} to compensate for different body sizes especially in comparative studies. The adaptiveness of different individuals, either of the same or of different species, can be compared but must be judged against the same selection force. This definition of the degree of adaptation is must useful for comparisons between closely related species and decreases in its usefulness as the degree of evolutionary relationship increases.

Energy utilization can also be used to indicate adaptive change as a feature requiring less energy would be better adapted. Thus *adaptation, the process,* is defined as *any evolutionary change in the form-function complex which reduces the amount of energy required by the organism to maintain successfully the synerg of the stated adaptation.*

The use of energy requirement to maintain the synerg as the measurement of the degree of adaptation is at least theoretically possible for any adaptation, and could be done at present for most structures of the skeletomuscular system, for example. The value of an independent measure of the degree of adaptation is that the adaptation can be measured independently of other evolutionary concepts such as fitness of the individual or survival of the species. If adaptation can be measured independently, then the contribution of the adaptiveness of a feature to the fitness of an individual or to the survival of the species can be ascertained. Questions, such as if an individual possesses a better adapted feature, will it have a greater fitness?, and how close is the correlation between the degree of adaptation and fitness?, can be answered only with an independent measure of the degree of adaptation.

Certain problems exist in the use of energy requirements to measure the degree of adaptation because this measure does not work in all cases. It is possible to provide examples in the skeletomuscular system in which one particular form-function complex is better adapted than another even though it would require more energy. Or to show examples of adaptive changes in a form-function complex that requires more energy. A simple example would be the length of muscle fibers within a muscle—longer fibers are needed if the muscle must shorten over a greater distance. Hence, if the selection force demands that the structure, for example, the tongue of a woodpecker, be moved over a longer distance, then a longer fibered muscle would be better adapted. However, a longer fibered muscle would require more energy when it contracts and shortens. In some cases, especially those adaptations associated with feeding, these difficulties could be overcome by regarding the degree of adaptation in terms of the energy acquired by the organism compared to the energy required; indeed such a measure is used by some ecologists. However, such a ratio would not work for all features and additional analysis is needed to develop a more comprehensive measure of the degree of adaptation. It does seem justified, however, to use the inverse relationship between energy requirement and the degree of adaptation in the large number of cases where it appears applicable. The ratio of energy obtained to energy cost can be used for judging the degree of adaptation associated with feeding. However in other cases some objective system of measure is needed to judge the benefit to the organism to be used in ratios of benefit obtained to energy cost for ascertaining the degree of adaptation.

Determination of Adaptations

Analysis of the form-function complex and its synergistic relationship to the environment makes it clear that a wide range of biological studies is needed for the determination of particular adaptations (Bock, 1978). None of these studies can be omitted and none can be done superficially. Adaptations can be ascertained only by direct analysis of the particular feature and its environment. Comparative studies are not valid for determining adaptations (Bock, 1977) as such methods depend upon causal laws explaining the correlations between environmental factors and adaptations. Such laws do not exist because the particulars of specific adaptations depend in part on their past history, and features with a partial historical, and hence chance-based, explanation cannot be explained by causal laws. Most morphological studies present a detailed anatomy and, more frequently in recent years, a good functional analysis of features but fail to include any observations of biological roles or of ecological factors. On the other hand, many ecological-physiological studies present thorough investigations of ecological and physiological factors and show what the adaptation must do, but stop short of identifying a particular feature as the adaptation and demonstrating its properties of form and function.

A wide range of laboratory and field studies are needed to demonstrate a particular adaptation as indicated in Fig. 9. Few complete studies of adaptations are available in spite of the great increase in functional morphological studies and of ecological investigations over the past quarter-century. The needed work can scarcely be carried out by a single investigator because of the extremely broad training required to undertake all facets of adaptational analysis. The most feasible approach appears to be by informal, flexible small teams which divide the work between laboratory analysis of descriptive and functional morphology and field investigations of biological roles and ecological factors (Bock, 1978). Information from both partners is needed to ascertain the nature of the synerg and of the adaptation. The project should be integrated from the onset with continuous feedback between the laboratory and the field work to permit follow-up on clues provided by different facets of the study. Details on problems associated with the analysis of adaptations can be found in Bock and von Wahlert (1965), Bock (1974, 1978), and in papers cited therein.

A special problem exists in studies of adaptation and of adaptive evolution in fossil organisms although the same exists for recent organisms which have not or cannot easily be studied in the field. Most evolutionary biologists believe that analysis of fossils provides the best basis to test explanatory models of macroevolution and the best examples of adaptive evolutionary change because of the time element available in the fossil record. Although it is clearly possible to test many aspects of organic evolution with observations from the fossil record, I doubt that it is possible to test concepts of adaptive evolutionary change with observations from the fossil record. The difficulty lies in ascertaining the adaptiveness of features observed in fossils which must be done prior to any comparisons made to test ideas of adaptive change. Determination of adaptations cannot be made with comparative methods and the necessary details of the environments of fossil organisms cannot be observed. If concepts of adaptive evolutionary modifications cannot be tested against observations from the fossil record, then it is doubtful that explanatory models of macroevolutionary change can be tested against fossil evidence. If this is true, it has serious consequences for the necessity of testing all facets of evolutionary theory against empirical observations because a major segment of evolutionary theory may be difficult to test.

Adaptation and Natural Selection

The concept of adaptation is intimately connected with the conception of natural selection. Adaptive changes can only occur under the action of selection. Hence an adaptive evolutionary change of a feature is one under the control of natural selection and an adaptive evolutionary change of a population would be one in which a feature is changing adaptively, that is, under the control of selection. It must be emphasized that not all evolutionary changes are adaptive nor must all adaptive changes be genetical changes. Many features can evolve nonadaptively, and even change considerably, as pleiotrophic byproducts of other adaptive evolutionary changes. Not all evolutionary changes in features must be adaptive. Intrinsic isolating mechanisms constitute a whole class of important evolutionary features whose evolution is nonadaptive (actually paradaptive). Almost all phyletic evolutionary modifications are adaptive, being under the control of selection. The only possible exception might be changes resulting from genetic drift (for example, associated with a few founder individuals), but these changes are almost always minor in terms of amount of phenotypic modifications and would soon be once again under the control of selection. Yet there is no reason to postulate that the occurrence of genetic drift means that selection is not operating because these two mechanisms are independent of one another. Genetic drift is simply one of the mechanisms whereby the genetically based phenotypic variation of a population is produced and made available for selection. It is highly doubtful that a nonadaptive change resulting from genetic drift would be freed of selection for more than a few generations if that long. Mechanisms of non-Darwinian evolution have not been supported by empirical observations.

Natural selection has been defined in many ways. The standard definition used in population genetics is *nonrandom differential reproduction of genes.* This is a *result* definition which describes the consequences of the action of certain causal mechanisms given particular initial conditions. Yet many evolutionary biologists use this definition *as if it is* *a causal selective mechanism.* They include as selection (a causal mechanism) any phenomena that may result in nonrandom differential reproduction of genes. Care must be taken to distinguish such phenomena, for example, selection of genes because of an altered genetical environment, from causal selective mechanisms which are restricted to synergical relationships between the external environment and the organism. Some uses of selection in quantum explanations of macroevolution, for example, species selection and internal selection, appear to be the result definition applied as a causal mechanism; these must be checked carefully. Any uses of natural selection other than as a causal mechanism arising from a synergical relationship between the external environment and the organism should be rejected. I will use selection only in this sense in developing an explanatory model of macroevolution.

Paradaptation

The concept of paradaptation was introduced to describe those aspects of a feature or those differences between features which are not associated with natural selection (Bock, 1967). Adaptive differences and aspects of features are associated with selection. However, evolutionary change is the result of the simultaneous action of two evolutionary mechanisms—the production of genetically based phenotypic variation and the action of natural selection. And not all differences and aspects of features can be described as adaptive. Those, which are under the control of genetical mechanisms, can be termed paradaptive because they are "besides adaptation," not being under the control of selection. The concept of paradaptation calls attention to the role of genetical mechanisms in evolution as the concept of adaptation calls attention to the role of environmental mechanisms. Because evolution is the consequence of the dual action of both mechanisms, features are simultaneously paradaptive and adaptive. They are adapted only if favored by selection (Fig. 8).

Preadaptation

A long standing dilemma in the adaptive explanation of the origin and further specialization of new features is how features could evolve under the control of natural selection when they first appeared and were too rudimentary to have any selective advantage. The argument has been offered that features could have a selective advantage when still very poorly developed and when their function and biological roles are not obvious. And, after all, extremely small selective advantages are amenable to selection and can be the basis of extensive change. But such arguments have never been convincing. The solution to this dilemma appears to lie in the concept of preadaptation (see Bock, 1959; Bock and von Wahlert, 1965:292).

Preadaptation refers to features that have acquired the necessary properties to be adaptive to a particular environmental demand before that demand and associated selection force has acted on the feature (Fig. 10). The concept of preadaptation has been associated with the notion of a change in functions ever since its proposal by Dohrn in 1875 (see Bock, 1959:200–201), yet it is clear that this use of function is in the meaning of biological role (Bock and von Wahlert, 1965:292). The definition of preadaptation advocated by Bock and von Wahlert (1965:292) is: *a feature is said to be preadapted for a new adaptation when its present form and functions permit the appearance of a new biological role and establishment of a new synergical relationship with the environment whenever the selection force for the new adaptation should arise.*

Evolution of a feature to the preadapted state is under the control of selection forces associated with the existing biological roles of the feature. Or it may be as a pleiotrophic byproduct of some other adaptive change. There is no reason to assume that evolution of a feature to a preadapted stage needs to be nonadaptive. Needless to say, the acquisition of any particular preadapted form by a structure is strictly fortuitous. Whenever a feature has reached the necessary preadapted stage, it is available to interact with the new selection force, establish a synerg, and become a new adaptation. The selection force may have been in existence and acting on the population before the preadapted stage is reached, or it may come into being after the structure reached the preadapted level. Evolutionary change from the preadapted stage to the adapted stage does not involve a change in form or functions, only the acquiring of a new biological role by the feature; hence, it is a nonhereditary evolutionary change. Preadaptation is frequently associated with a non-utilized function of the feature. The new adaptation may be a relatively poor one and usually requires considerable postadaptive change to develop a more perfect correlation between the biological role and the selection force—a synerg requiring less energy.

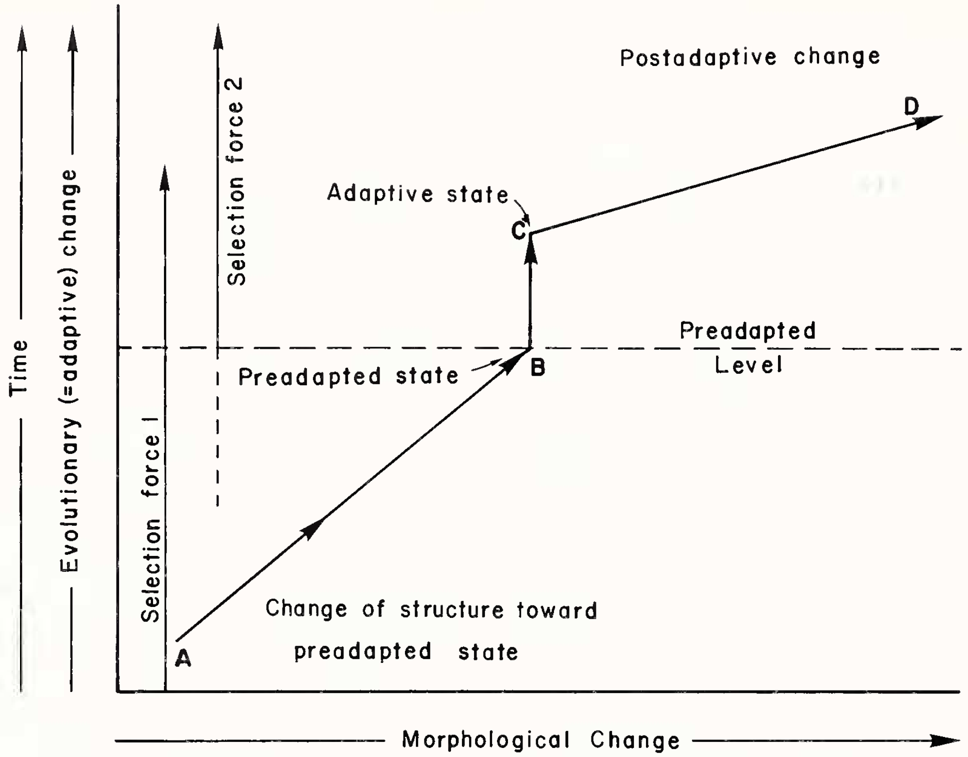


Fig. 10.—Schematic diagram to show the evolution of a new adaptation via a preadapted stage. The horizontal axis indicates morphological change. Time and evolutionary change are shown along the vertical axis. Evolution of the feature to the preadapted state (B) is under the control of selection force 1. When selection force 2 forms a new synerg with the feature at B, the feature shifts to a new adaptive state (C) from which it can undergo a period of postadaptive change toward D (taken from Bock, 1959:Fig. 5).

The origin of new features via a preadapted stage solves the dilemma of the selective value of the new feature at a time when it is too poorly developed to have the needed function and biological roles. Evolution of the feature up to the preadapted level occurs under the action of the old selection forces, not the new selection force associated with the new adaptation.

The notion of preadaptation has a second advantage in that it solves the dilemma of the necessary perfection of adaptations (Frazzetta, 1975), for example, the biomechanical interaction of skeleto-muscular systems, during their origin and early evolution when they are not sufficiently developed. I accept the notion that features can be far less than well-integrated, perfected systems and can still be adapted. A period of postadaptive specialization usually follows the appearance of any new adaptation. Yet, some degree of perfection as discussed by Frazzetta (1975) is required which is achieved by the preadapted step.

A SYNTHETIC MODEL FOR MACROEVOLUTIONARY EXPLANATION

The proposed synthetic model to explain macroevolutionary modification must have a number of properties to be a fully reductionistic one. The model must permit adaptive change throughout with selection acting on the evolving population at all times. No jumps or discontinuities of a level greater than those observed between successive generations of the same phyletic lineage can exist. The possible sources of the needed directional selection must be identified. Only those evolutionary mechanisms known to operate on the microevolutionary level can be used; no special macroevolutionary mechanisms are permitted. These mechanisms are those of speciation (=splitting of phyletic lineages)

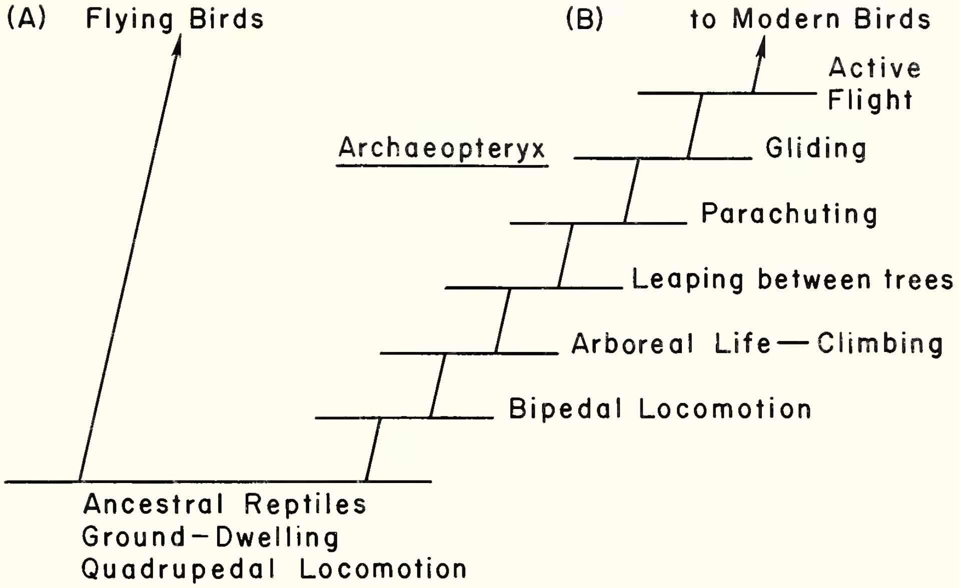


Fig. 11.—Schematic diagrams contrasting two different models of steps in the origin of new taxa. (A) A single-step change from ground-dwelling reptiles to flying birds; the selection forces responsible for this change are associated with flight. (B) A series of stepwise evolutionary changes from reptiles to modern birds; only the major levels have been included. In this model, a series of selection forces are responsible for the total change; each set of forces is associated with the corresponding level of change (taken from Bock, 1965:Fig. 1).

and, most importantly, those of phyletic microevolution. The latter mechanisms are those which have been tested against observations resulting from experiments of population geneticists and from the work of animal and plant breeders. The mechanisms of speciation and of adaptive phyletic evolution (plus pleiotrophic byproducts) discussed above are sufficient for all macroevolutionary explanation. Changes on the microlevel must be summed properly to achieve the major evolutionary modification. This summation must be an exact chronological one with evolutionary events at one point in time setting the stage for those at the next step in the sequence. The critical conceptual transformation in the model is that from a horizontal to a vertical comparison or vice versa depending on how the explanation is being developed. If a sequence of adaptive vertical steps is postulated for phyletic evolution within a single lineage, it can be tested, with extremely rare exceptions, only against a series of observations made in a horizontal comparison across many different phyletic lineages. Although the differences observed in the pseudophylogeny comprised of the steps in the horizontal comparisons may have other than an adaptive explanation, they must be assumed to be adaptive so long as this assumption is a reasonable one.

Model for Major Adaptive Shift

The first step is to develop an overall model which provides the framework for the whole explanation and the basis to focus discussion on the crucial points. The model to be used is one I advocated earlier (Bock, 1965) using the evolution of birds as the example. Although the model will be discussed in terms of the evolutionary origin of a new major taxon—the class Aves—it is equally suitable for explanation of the evolution of a single feature.

Any change from the ancestral to the descendent group involves a sequential series of many steps, each representing an intermediate stage between the old and the new adaptive zones (Fig. 11B). The notion of a single step between the ancestral and descendent groups (Fig. 11A) is not supported by any positive observations. The major difference between these contrasting models is that only one set of selection forces is involved in the one step model while a sequence of different selection forces is involved in the multiple step model. The steps must be in proper chronological order with evolutionary modifications at one step setting the stage for the changes at the next. Each step in the series may include preadaptations and perhaps key innovations as well as a period of postadaptational adjustment. During the postadaptational period, the newly

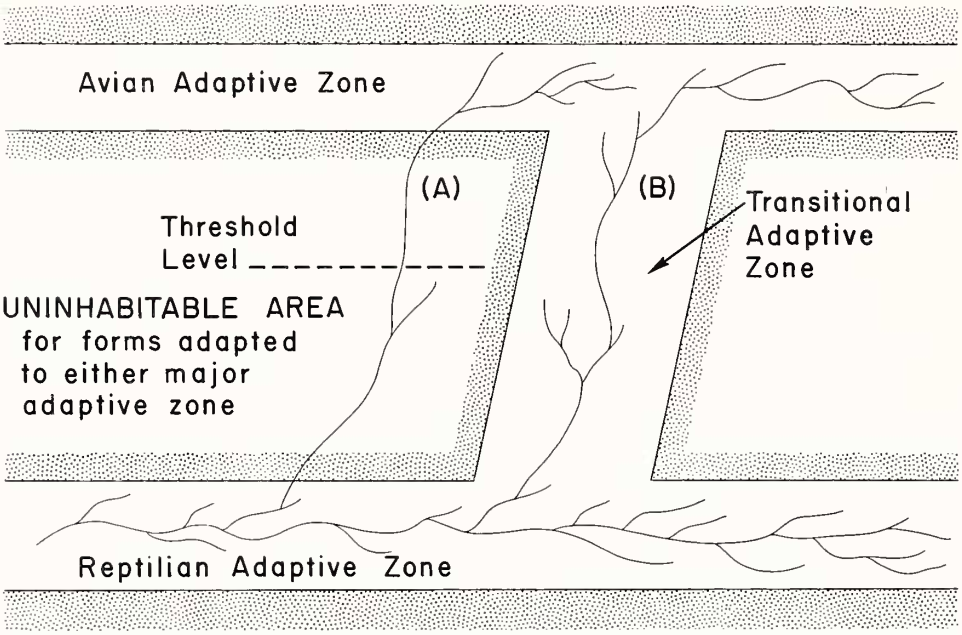

Avian Adaptive Zone
(A)
(B)
Threshold Level
Transitional Adaptive Zone
UNINHABITABLE AREA for forms adapted to either major adaptive zone
Reptilian Adaptive Zone

Fig. 12.—Schematic diagrams contrasting two different models of crossing from one major adaptive zone to another. (A) The phyletic lineage must cross an ecologically unstable region which may be considered as a threshold. (B) The phyletic lineage crosses from one major adaptive zone to another through a transitional adaptive zone. In these models, the region between the major adaptive zones is regarded as uninhabitable for organisms adapted to either major adaptive zone (taken from Bock, 1965:Fig. 2).

evolved features are integrated with earlier changes so that the resulting adaptations are dependent on the entire complex of interdependent features. The individuals of the evolving population are always integrated wholes adapted to their environment. Changes appearing at each level in the sequence are dependent on those features that had evolved at previous levels. Thus, flight with an aerodyanamic surface formed by elongated strengthened feathers attached to the posterior edge of the forelimb is dependent upon the earlier evolution of feathers.

In the evolution of flying birds from terrestrial reptiles, the steps would include bipedal locomotion, climbing, leaping, parachuting, gliding and finally active flight. Various features of the ancestral reptiles would have evolved at different times and at different rates in response to the selection forces associated with each step; these changes would occur in a very definite sequence depending upon the features, their somatic interactions and mechanisms of internal adjustment, and the organisms. The resulting pattern of change is stepwise or mosaic evolution (de Beer, 1954). Discussion of the details of mosaic evolutionary change in the evolution of birds is beyond the scope of this paper. Suffice it to say, *Archaeopteryx* exhibits a mosaic of characters, some very reptilian, a few as fully developed as those in modern birds and others at various intermediate stages.

The evolution of each new major feature or modification must be subdivided in like fashion into a series of steps as has been done for the avian feather by Regal (1975).

Functional significance of each morphological change and feasible biological roles must be discussed together with possible environments and selection forces. Thus, feathers may have a number of functions, two of which are temperature regulation and providing an aerodynamic surface. Each could be associated with biological roles having a synergistic relationship with a selection force that could have been responsible for its origin. Choice of temperature regulation as the most reasonable function associated with the origin of feathers is based on a number of considerations involving the biology of the whole organism, not just the feathers. Yet, this does not solve questions of the biological roles of temperature regulation, the environmental factors and the exact nature of the selection force. A decision that selection forces associated with arboreal life were central to much of the evolution of birds from reptiles does not mean that the transi-

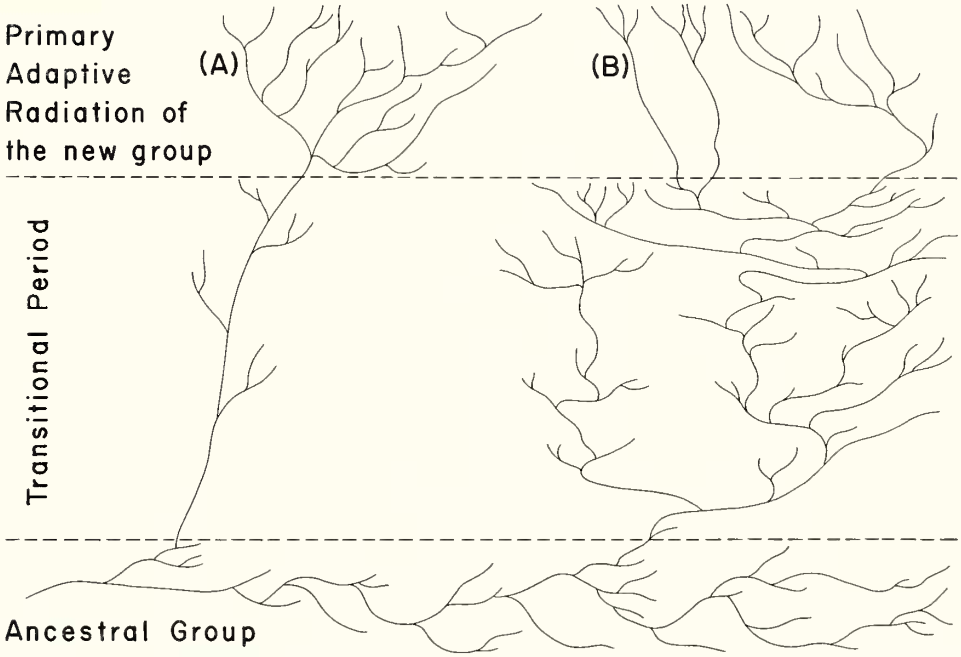


Fig. 13.—Schematic diagrams contrasting two different models of the number of phyletic lineages involved in the origin of a new group of organisms. (A) A single phyletic lineage with a few insignificant side branches leads to the new group. The primary adaptive radiation stems from this single line after the basic features of the new group have evolved. (B) Several phyletic lineages with successive series of adaptive radiations lead to the new group. Several different lineages may contribute to the primary adaptive radiation of the new taxon. The second model emphasizes that evolution of a new taxon involves successive series of adaptive radiations with a number of coexisting phyletic lineages at any point in time rather than a single lineage (taken from Bock, 1965:Fig. 3).

tional protoaves lived only in trees. It is entirely possible for these animals to spend part of their life on the ground as active bipedal predators and part of their time in the trees as a place to rest and to reproduce, that is, incubate their eggs and raise their young in a nest placed in a tree.

The pattern of selection forces acting during the period of a major evolutionary change and the nature of the intermediate environmental zone are crucial for the general model.

Adaptive Zones

The concept of adaptive zones or adaptive peaks has proven to be quite useful except for the ambiguous "regions" between the adaptive zones. Simpson (1953:201–202, and elsewhere) regards these intermediate areas as "discontinuities or essentially unstable ecological zones" that must be crossed when a group evolves toward another adaptive zone and new higher taxon (Fig. 12A). This concept gave rise to the notion that the phyletic lineage is in an inadaptive phase of evolution while passing through this region. Selection is regarded to be severe and the population in the intermediate area is evolving rapidly compared to selection and rates of evolution in the normal adaptive zones. The discontinuity between the two adaptive zones has been described as a threshold level that the evolving population must surmount. If it fails to do so, it either falls back to the old adaptive zone or becomes extinct.

No real evidence supports the concept of unstable areas between adaptive zones which can be regarded as uninhabitable areas for the organisms in either neighboring adaptive zones.

Crossing from one adaptive zone to another is via a transitional zone that extends between the two major zones (Fig. 12B). These transitional zones may be temporary, appearing and disappearing as ecological conditions change. However, some transitional zones may remain in existence for extremely long periods of geological time and others may be as permanent as the major adaptive zones. The last may be the most frequent. A population in a transitional zone is fully adaptive to the ecological conditions there and does not experience selection forces of greater magnitude than those operating in the major adaptive zone. The only difference may be that the selection in the transitional zone may be

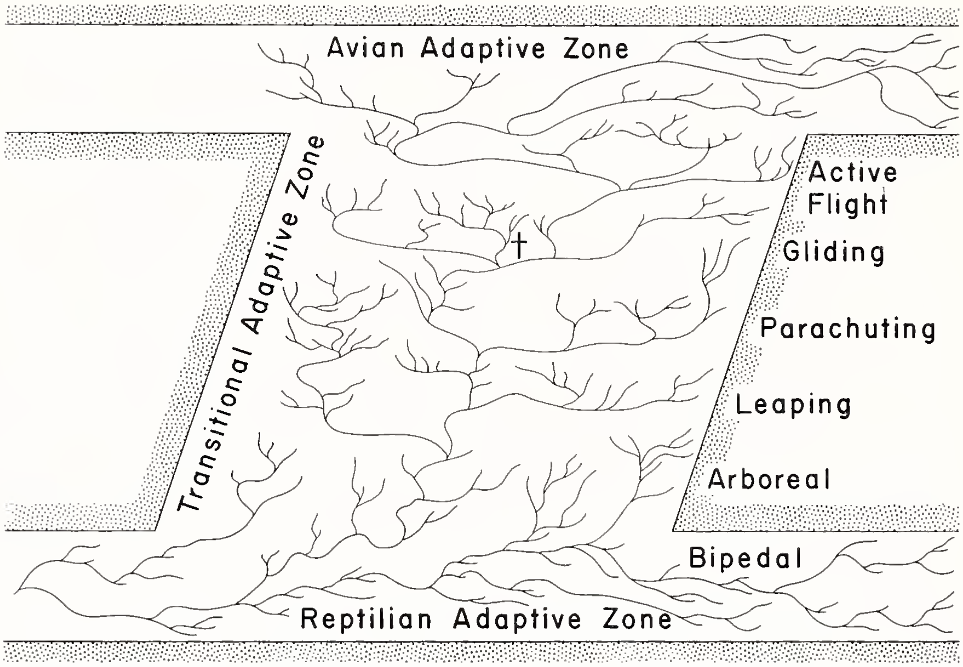


Fig. 14.—A composite model for the adaptive origin of a new group of organisms, in this case the evolution of birds from reptiles. The successive radiations seen in the transitional adaptive zone form a pattern of stepwise evolutionary levels indicated on the side of the transitional zone. The approximate position of *Archaeopteryx* is indicated by a cross (†). Relative widths of the major and transitional zones, sizes of the various radiations and relative times are not shown to correct proportions (taken from Bock, 1965:Fig. 4).

more strongly directional than that in the adaptive zone.

Number of Lineages

It has generally been assumed that a single phyletic lineage, or a small number at most, are involved in the origin of a new taxon (Fig. 13A). This concept developed because of the small number of fossils available to trace the change from one group to another. In the average case, scarcely enough fossils exist to fill the gaps in a single phyletic lineage. But the small number of known fossils associated with the origin of any group is probably a consequence of the speed of the change compared with the "time intervals" of the fossil record.

Although little supporting evidence is available, it seems reasonable to assume that several to many phyletic lines are involved in major evolutionary changes and that a series of small radiations are present throughout the transitional period (Fig. 13B). These small radiations replace one another and may correspond to the sequential stages shown in Fig. 11B. This is the pattern shown by the evolution of mammals from the therapsids and by the evolution of horses. It is not in conflict with any positive paleontological data and is in close agreement with the concepts of mosaic evolution and of transitional adaptive zones and with the pattern of diversification shown by recent groups of organisms.

One difference between these two concepts is that in the single lineage model, adaptive radiation occurs after the lineage enters the new adaptive zone and is suggested to be a mode of evolutionary change different from that responsible for the origin of the group. In the multiple lineage model, adaptive radiations occur during the entire transitional period with perhaps the only difference being one of magnitude of the radiations—those in the major adaptive zones being larger.

The Combined Model

The model for the sequence of events involved in the origin of new groups is simply a combination of the several models shown in the previous figures (Figs. 11B, 12B, and 13B). The composite model is illustrated in Fig. 14 by the evolution of birds.

The ancestral group evolves through time but remains within its adaptive zone. New adaptive radiations occur and new forms appear. These refill the zone again and again to replace the lineages that

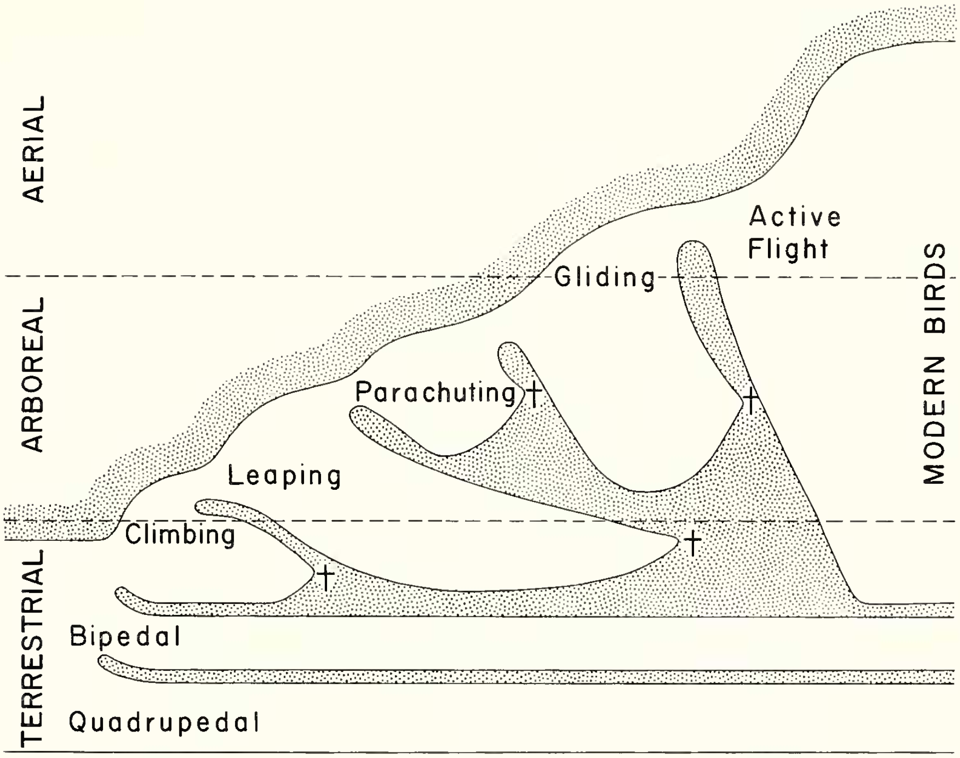


Fig. 15.—A schematic model showing a possible pattern of radiations of the different stages in the evolution of birds through three major adaptive zones—terrestrial, arboreal, and aerial. Sizes and durations of the radiations and the times of extinction are strictly hypothetical. Blank areas inside the stippling are successive adaptive levels. It may be seen that each successive radiation and resulting adaptive radiation did not remove the descendent forms from competition with their ancestors. This model suggests that the radiation at any level would probably continue as long as it did not give use to a higher (better adapted) level (taken from Bock, 1965:Fig. 5).

have died out, but the basic organization of the group remains the same, just as the zone remains the same. The mechanism for the adaptive radiations involves preadaptations, key innovations, postadaptational change, and others as outlined above. The size of the group expands and shrinks as the zone becomes wider and narrower.

The start of evolution toward a new group begins with radiation into an intermediate zone. These radiations continue as long as the intermediate zone continues to exist, and are under the control of the same evolutionary mechanisms that acted earlier in the ancestral adaptive zone. Similar patterns of preadaptations, key innovations and postadaptation occur with the only difference being directional selection acting on the lineages in the transitional zone. The appearance of a new adaptive zone depends to a great extent on the features that appeared, by chance, in the intermediate group. A number of arboreal and even gliding lines appeared in the reptiles, but only one—that leading to birds—possessed the adaptations permitting successful invasion of the new (aerial) zone. Yet, the ecological habitat of open air had existed long before birds evolved.

Extinction of earlier radiations in transition is not because of the nature of the transitional ecological zone but because of the appearance of later radiations (Figs. 15 and 16). As these subsequent radiations appear, the later forms often inhabit the same ecological zones and thereby compete with members of the earlier radiations. If the changes leading to modern birds are shown against three major adaptive zones—terrestrial, arboreal, and aerial—it can be appreciated that members of later radiations are not removed from competition with those of earlier radiations. Species that can leap between trees are still arboreal and will compete with those arboreal species that can only climb. Leaping from tree to tree would be a definite advantage. Later species that could parachute and still later ones that could glide are still arboreal dwellers, but have decided advantages over those that are only able to leap from tree to tree. Competition

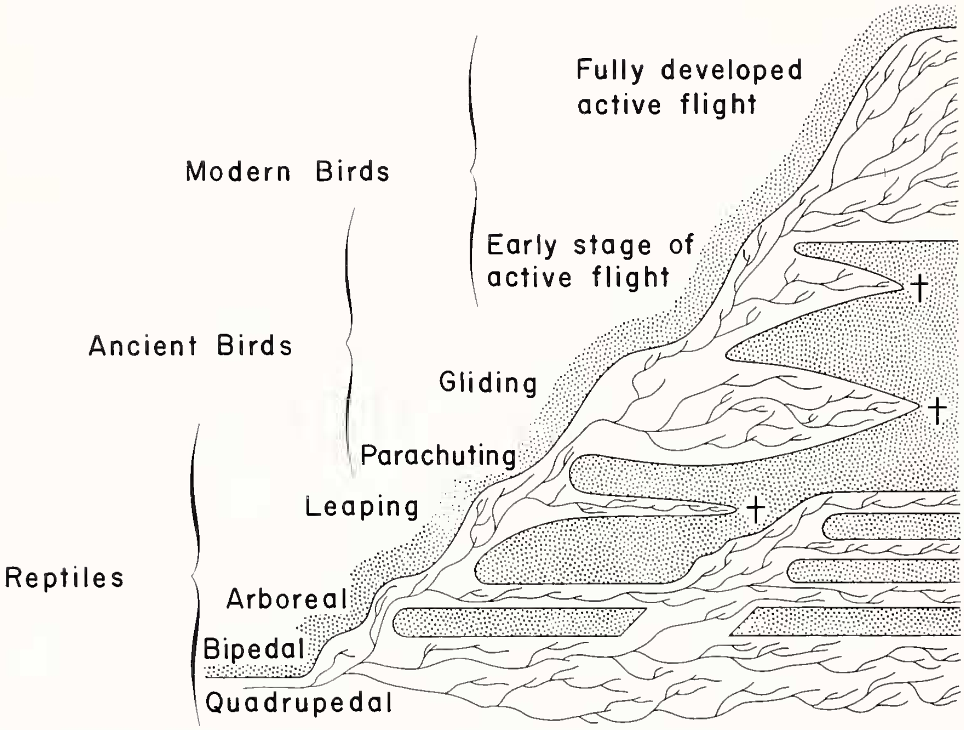


Fig. 16.—A schematic model showing the different stages in the evolution of birds through successive taxonomic groups—reptiles, ancient birds, and modern birds. The possibilities of transitional zones appearing several times and of their continued existence, for example, at the arboreal and leaping levels, are emphasized in this model. Moreover, the model illustrates the severe selection pressure exerted by flying birds on other arboreal groups that may be evolving fully developed aerial adaptations (taken from Bock, 1965:Fig. 6).

between members of different radiations and the usual extinction of the earlier radiations produces the distinct gaps seen between most major taxa. And it may be a significant factor in the usual lack of fossil record of transitions between major groups.

Selectional Sources

Adaptive evolutionary change requires strong directional selection acting over a long period of time. Not even advocates of quantum theories deny this requirement as they rely heavily on selection for much of macroevolution even if a saltation or a period of no selection is included. Moreover, the directional selection must be able to explain the pattern of mosaic evolution that is characteristic of major evolutionary modifications. Thus, directional selection must not only be strong and continuous for a long period of time, but the individual selection forces must act at different times and at varying rates during the intermediate period.

Most workers have not attempted to identify the source of the needed directional selection or assume it to be from the physical environment or from obvious factors as food, shelter, locomotion, and others. I advocated first in 1970 and more fully in 1972*a* that the major source of directional selection pushing a major evolutionary change came from species interactions of all types (see Darwin 1859:487–488). Advocating selection from species interactions as the driving selection for macroevolution does not gainsay the continued action of selection from the physical factors of the environment. These exist and control the evolution of many features of the organism. Selection from species interactions overlies these other selection forces and is almost always the major part of selection responsible for major change. I do not want to leave the impression that selection from species interactions is not important in microevolutionary events, in speciation and in continued evolution within the limits of a taxon remaining in its major adaptive zone. Such selection is also very important there as it is a major component of the total selection acting on all species.

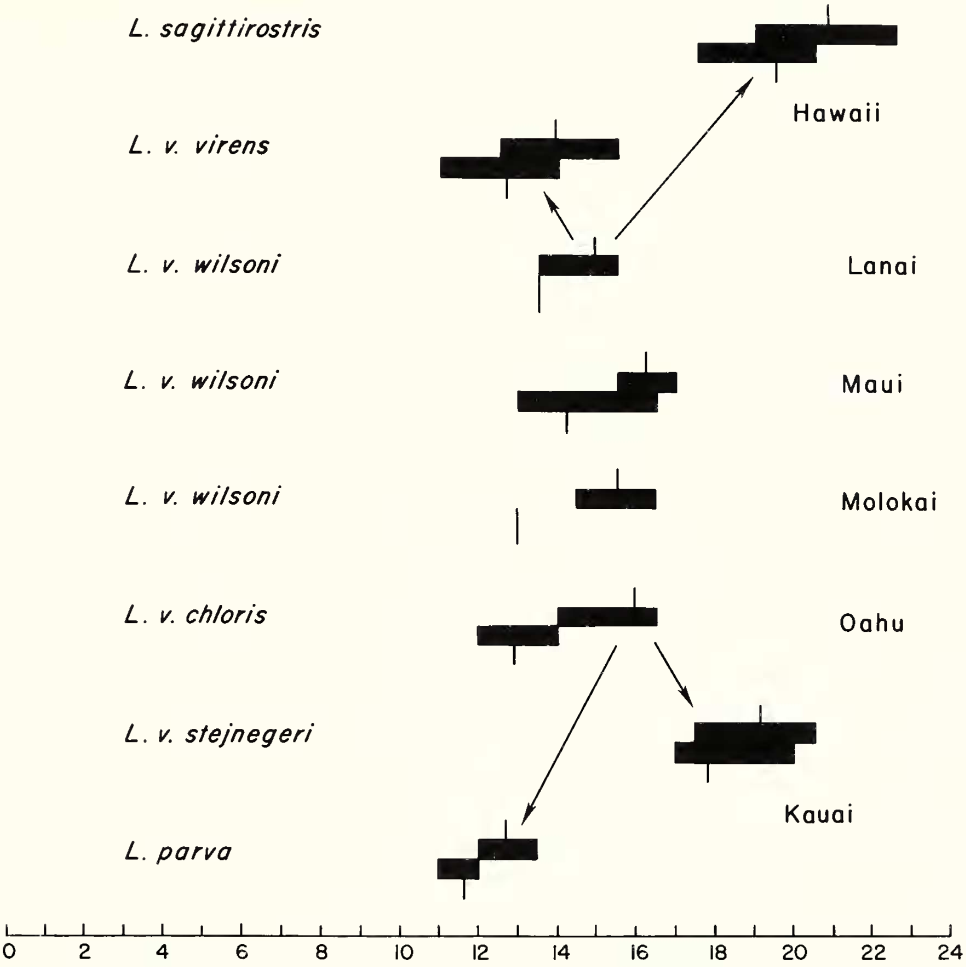


Fig. 17.—Bill length (culmen in mm) of the *Loxops virens* complex to show geographic variation and displacement); data taken from Amadon (1950). Range is indicated by the solid bar, the mean by the vertical line, males shown by the upper bar and females by the lower (taken from Bock, 1970:Fig. 4).

Species interactions can be classified into two major categories—namely, (a) *exclusionary* interactions, including ecological competition and reproductive efficiency (reduction of reproductive cost by improving means of species recognition and other types of intrinsic isolating mechanisms of low reproductive cost); and (b) *coevolutionary* interactions, including predator-prey, parasite-host, and flower-pollinator relationships and all other sorts of symbiotic associations.

Species interactions and the resulting directional selection force are dependent on the coexistence of the interacting species and will result in modification of at least one and usually all of the interacting species. Selection is mutual because each of the interacting species exerts selection on the other; unidirectional selection is extremely rare if it occurs at all. The two types of species interactions are different in their mode of action, in the mode and strength of selection, and in the pattern of evolutionary change of the interacting species. Other than the broadest generalizations that species interactions result in mutual selection and that the strength and complexity of the selection increases with the number of interacting species, no generalizations can be offered on the mechanism of the interaction, the nature of the resulting selection and the pattern of the evolutionary change.

Exclusionary species interactions include ecological features associated with competition and/or ethological features (and all other intrinsic isolating mechanisms) associated with reduction of reproductive wastage (Bock, 1970:706) in pairs of species that are already reproductively isolated. Each

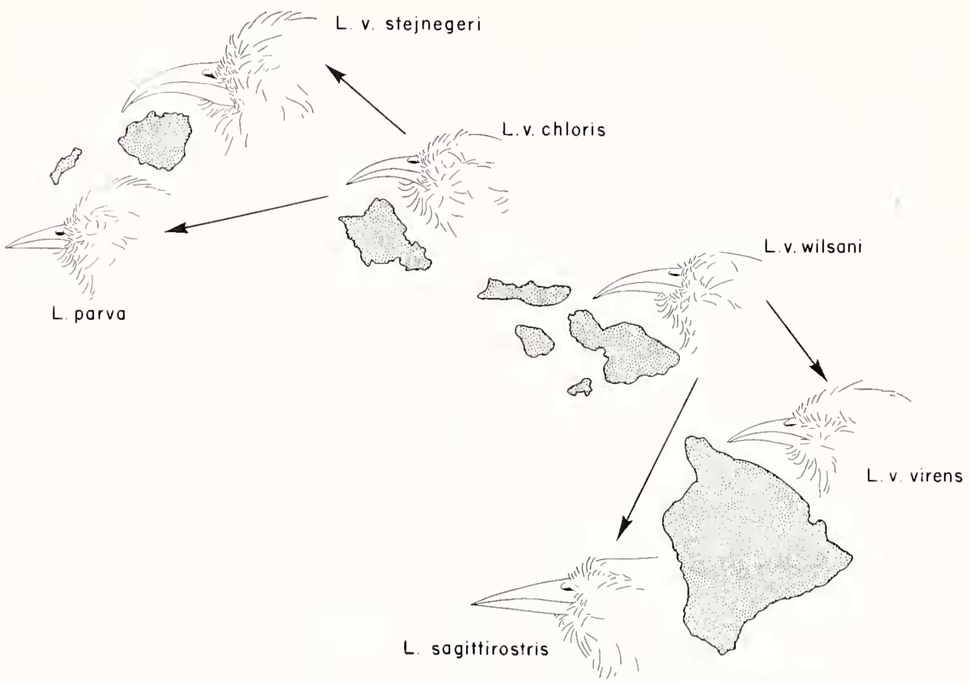


Fig. 18.—Double invasion and character displacement in bill length and shape in the *Loxops virens* complex on Kauai (*v. stejnegeri* and *parva*) and on Hawaii (*v. virens* and *sagittirostris*) to illustrate the consequence of exclusionary species interaction. See Fig. 17 for details in displacement of bill length (taken from Bock, 1970: Fig. 5).

species will exert selection on the other with possible evolutionary consequences ranging from the extinction of one species to character divergence in both (Lack, 1944, 1947). Exclusionary species interactions are usually most intense between two newly evolved sister species during the sympatric phase of speciation, but may be strong between very distantly related species. The introduction of trout into New Zealand resulted in serious decline in the native Blue Duck (*Hymenolaimus malacorhynchos*) because of competition for the same food—aquatic insect larvae (Kear and Burton, 1971). In the Hawaiian honeycreepers (Drepanididae) exclusionary species interactions occurred between sister species (for example, between *Loxops v. virens* and *Loxops sagittirostris* on Hawaii and between *Loxops v. stejnegeri* and *Loxops pava* on Kauai; see Figs. 17 and 18; Bock, 1970:711) and between closely related genera (for example, between *Loxops v. stejnegeri, Hemignathus lucidus hanapepe,* and *Hemignathus procerus* on the island of Kauai; Bock, 1970:714–715). Lack (1947) provided the classic example of how bill size shifts in the sympatric species of *Geospiza* and *Camarhynchus* (the Darwin's finches) depending on which of the congeneric species are present on each island.

The consequence of exclusionary species interaction of greatest significance for macroevolution is character displacement. The two interacting species will diverge from one another under the action of the mutual selection thereby reducing the degree of interaction and hence the strength of directional selection. Once interaction ceases between the species pair, further divergence will be greatly reduced or cease totally until another cycle of speciation occurs or until another species invades the range of one of the two original species. Selection from exclusionary species interaction is frequently very strong at the onset, but is quickly reduced and is of short duration. It depends upon repeated speciations to maintain a high level of selection.

Coevolutionary species interactions involve a number of different types such as predator-prey relationships, pollinating organisms, and symbioses (Ehrlich and Raven, 1965; Ehrlich, 1970). This category of interaction is characterized by a direct utilization by one member of the species pair of resources of the other. In some cases, both members of the pair use resources of the other species, but generally in quite different ways. The only requirement is that use of at least one member of the spe-

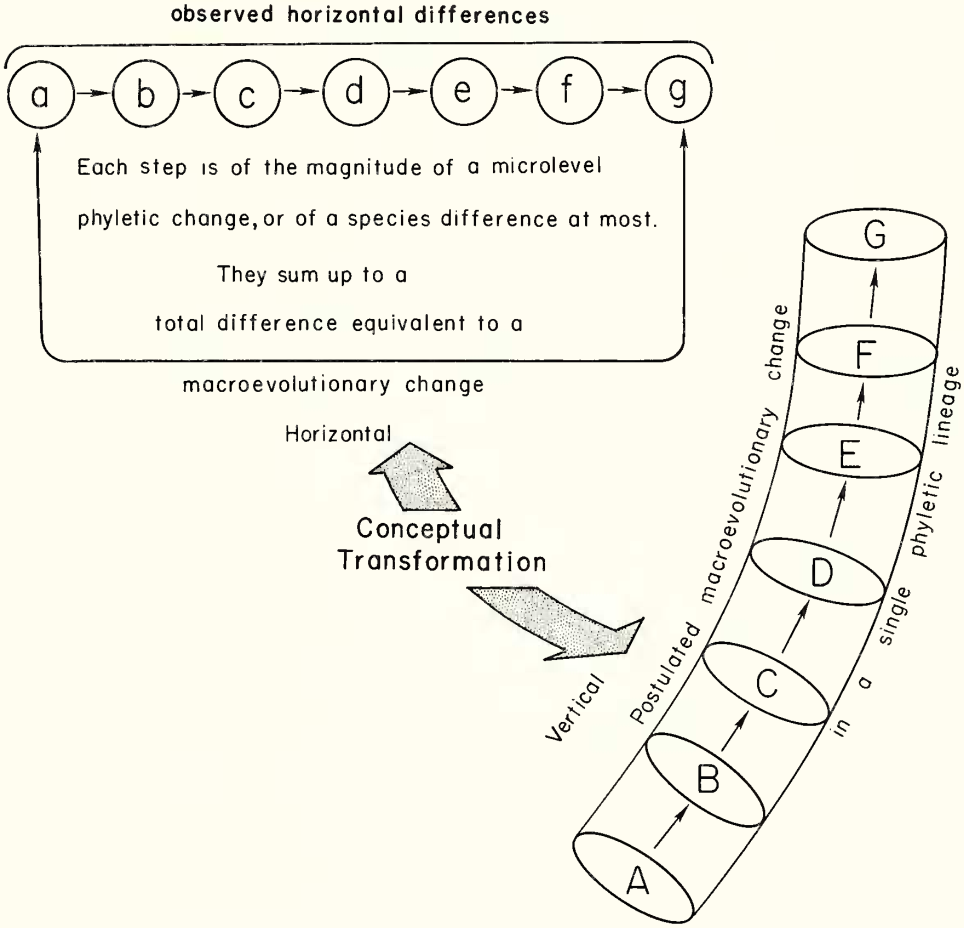

observed horizontal differences
a
b
c
d
e
f
g
Each step is of the magnitude of a microlevel phyletic change, or of a species difference at most.
They sum up to a total difference equivalent to a
macroevolutionary change
Horizontal
Conceptual Transformation
Vertical
Postulated macroevolutionary change in a single phyletic lineage
A
B
C
D
E
F
G

Fig. 19.—Schematic diagram to show the conceptual transformation from a vertical series of changes in a phyletic lineage to an analogous pseudophylogeny of horizontal steps. The horizontal comparison is the sequential species analysis that serves to test the macroevolutionary modification through a successive series of small steps each of which can be explained by the known mechanisms of phyletic microevolution.

cies pair must be advantageous to the other; in symbiosis, both species gain an advantage. In every case, each species exerts selection on the other no matter which one is actively utilizing the other. The result of the mutual selection is modification of one or both species, but this evolutionary change is usually not a divergence as in the case of exclusionary interactions. Generally, both species change with the ensuing modification resulting in only a temporary reduction, if any, of the selection being exerted. The general consequence of coevolutionary interactions is continued evolution of both interacting species as each of the species changes. Coevolutionary interaction is an "arms race" type of evolutionary interaction as each species must continue to evolve to keep abreast of the evolutionary changes of the other. It is not possible to win in coevolutionary interactions except temporarily or in the case of extinction of the other species.

Coevolutionary species interactions probably involve weaker selection than exclusionary interactions, but the strength of selection need not decrease with evolutionary change and the interaction continues for much longer periods of time. Coevolutionary interactions do not depend upon continued speciations and may be especially important in macroevolutionary change of taxonomically isolated species and of single taxa evolving on isolated islands.

An important aspect of selection arising from species interactions is that it modifies as the interacting species evolve under the control of the mutant selection. This would produce the pattern of changing selection forces needed for mosaic evolution.

Both types of species interactions, but especially exclusionary, provide the link between the species and speciation and macroevolutionary change. With increased speciation and greater number of species, more species interactions will occur and with them more directional selection to drive macroevolutionary change. Thus, it is not speciation itself that is essential to macroevolution, but the resulting species interaction and the mutual directional selection that helps to drive macroevolution.

Sequential Species Analysis

The model presented above shows that macroevolution can be explained as adaptive evolutionary change with the major driving directional selection arising from species interactions of all sorts. Yet, the unit changes that comprise a major evolutionary modification do not have to be ones at the microevolutionary level. The model as proposed thus far is completely consistent with the hypothesis that the evolutionary steps are of a larger magnitude than those observed at the microlevel—that is, the hypothesis of quantum jumps. It is possible to postulate a mechanism of quantum evolutionary jumps that is fully adaptive. The concept of systemic mutations proposed by Goldschmidt (1940:206) is consistent with theories of adaptive macroevolution. It is necessary to show that major evolutionary change can be explained fully as a series of sequential changes, each of which is at the level of microevolutionary change as studied by population geneticists and by plant and animal breeders. I discussed the role of sequential species analysis under the heading of microevolutionary sequences (Bock, 1970) and of sequential species analysis (Bock, 1972*b*). The concept of sequential species analysis is that a horizontal comparison of differences between species and subspecies may be postulated to be equivalent to the sequence of microevolutionary steps in a macroevolutionary change. A conceptual transformation must be made between the horizontal comparison of observed differences between species and the postulated macroevolutionary change in a single phyletic lineage (Fig. 19).

The synthetic explanation of macroevolution states that the sequence of modification in a particular phyletic lineage that is large enough to be termed a major evolutionary change can be explained fully by microevolutionary mechanisms. No special evolutionary mechanisms are needed in which case macroevolutionary explanation has been reduced fully to microevolutionary explanation. The macroevolutionary change is the difference between A and G shown in the phyletic lineage in Fig. 19. This change is the result of the chronological series of microevolutionary steps A → B, B → C . . . F → G shown. The populations A B . . . G are successive cross-sections of the phyletic lineage, which are chosen for the purposes of the explanation.

The major evolutionary change to be explained is one of phyletic evolution and hence, it is to be reduced to the mechanisms of phyletic evolution—the formation of genetically based phenotypic variation and natural selection. As change is being traced only along a single phyletic lineage, we are not concerned with the number of lineages that may have split off of the phyletic lineage A–G. Hence, the mechanisms of speciation do not apply at all—they are not part of the needed explanation. *A full reductionistic explanation of macroevolution does not include the mechanisms of speciation.* Speciation, or the splitting of phyletic lineages, results in a multiplication of species. The role of species in macroevolution is they provide mutual species interactions (exclusionary and coevolutionary) and hence mutual selection. The more species existing, the greater will be the selection from the species interactions and the greater will be the driving force of the macroevolutionary change.

Given a macroevolutionary change to be explained with a known starting point and a termination, the first step would be to establish a plausible phylogenetic sequence of changes. If the evolution of a new feature is being analyzed, then the phylogenetic sequence will be of stages associated with this feature. If the evolution of a new major taxon is being examined, then it may be sufficient to limit discussion to the sequence of individual features associated with the origin of the group. Establishment of the phylogenetic sequence depends upon consideration of evolutionary mechanics of individual features, functional and evolutionary interactions of morphological components of functional complexes, organism-environmental interactions, behavior and ecological factors, and whatever else may bear on it. The steps in the sequence should be as small as possible without the total number becoming unreasonably large.

At this point the conceptual transformation must be made from the vertical phylogenetic sequence to a corresponding horizontal series. The species in the horizontal sequence and the differences between adjacent members provide an analogy of the sequence of changes that took place in the phylogenetic lineages. Each step between adjacent members should be of a magnitude and type corresponding to those demonstrated in animal and plant breeding or in experimental work in population genetics. The difference between the ends of the horizontal sequence is assumed to be summation of the small individual differences and to correspond to the macroevolutionary change to be explained.

It must be emphasized that horizontal comparisons are not comparable to vertical ones. Also, it is not possible to equate all horizontal differences or similarities with corresponding vertical differences or similarities. Interpretations reached after a horizontal comparison cannot be automatically extrapolated to vertical comparisons. Yet, the conceptual transformation between a vertical phyletic lineage and a horizontal series of species must be made if one wishes to continue analysis of macroevolution regardless of whether one advocates quantum theories or reductionary theories. This transformation is a scientific hypothesis that must be tested against empirical observations. The nature of the tests is obvious. One must observe actual phylogenies and compare these to corresponding horizontal series. The only phylogenies that are readily available are those from plant and animal breeding. Some of these may not be suitable for tests because of missing information. Examples of tests could be a comparison of the sequence of changes in the history of dog breeding with the types and magnitude of differences between breeds of dogs. Another would be the work done with fruit flies. I will accept that tests can be made of the transformation hypothesis and that these tests will not disprove the hypothesis although I cannot detail any good tests at this time. The actual testing of the transformation hypothesis is of key importance.

If the steps in a phyletic sequence of a macroevolutionary change correspond to an analogous horizontal series and if the observed differences between all adjacent species in the horizontal series are of the magnitude demonstrated in phyletic modifications in plant and animal breeding and in experimental population genetics, then it can be concluded that the modifications along the phyletic lineage are of this magnitude and can be explained by the known microevolutionary mechanisms of phyletic evolution. If the total difference between end members of the horizontal series is the summation of the individual small differences between adjacent species and if this total difference corresponds to a major evolutionary change, then it can be assumed that the major phyletic evolutionary change is the summation of a chronological series of small phyletic modifications. These assumptions can be made because of the possibility of a conceptual transformation between a vertical phyletic sequence and a horizontal "pseudophyletic" series.

If the macroevolutionary modification can be shown to be a summation of a sequence of small steps each of which can be explained by known mechanisms of phyletic microevolution, then the macroevolutionary change is completely explained by these mechanisms of phyletic evolution on the microlevel. No additional mechanisms are required. Macroevolutionary explanation has been reduced to microevolutionary explanation. Thus, phyletic evolutionary change of all magnitudes is explainable with the same set of causal mechanisms which has been one of the long cherished hopes of evolutionary biologists.

Methods of Testing

Scientific theories, hypotheses, and explanatory models are easy to postulate and have little value unless methods are outlined by which they can be tested. And successful testing increases their value. A major failure of most explanatory theories of macroevolution has been the lack of suggestions of how these theories are to be tested or improper testing.

Most workers have attempted to test particular or conflicting sets of macroevolutionary explanations against evidence from the fossil record. Unfortunately, such tests are invalid for several reasons. First, the degree of resolution of geographical distribution of species, including isolates, and of temporal change in the fossil record is simply not fine enough to correspond to microlevel steps in macroevolutionary changes. The necessary level of knowledge of geographical distribution is known only for a few groups of recent organisms, such as birds and mammals, and not even completely for these groups. Important changes for macroevolution can occur in less than 5,000 years and probably in less than 1,000 years. Such time intervals are simply too small to be resolved in the fossil record—they are geologically instantaneous. Second, it is

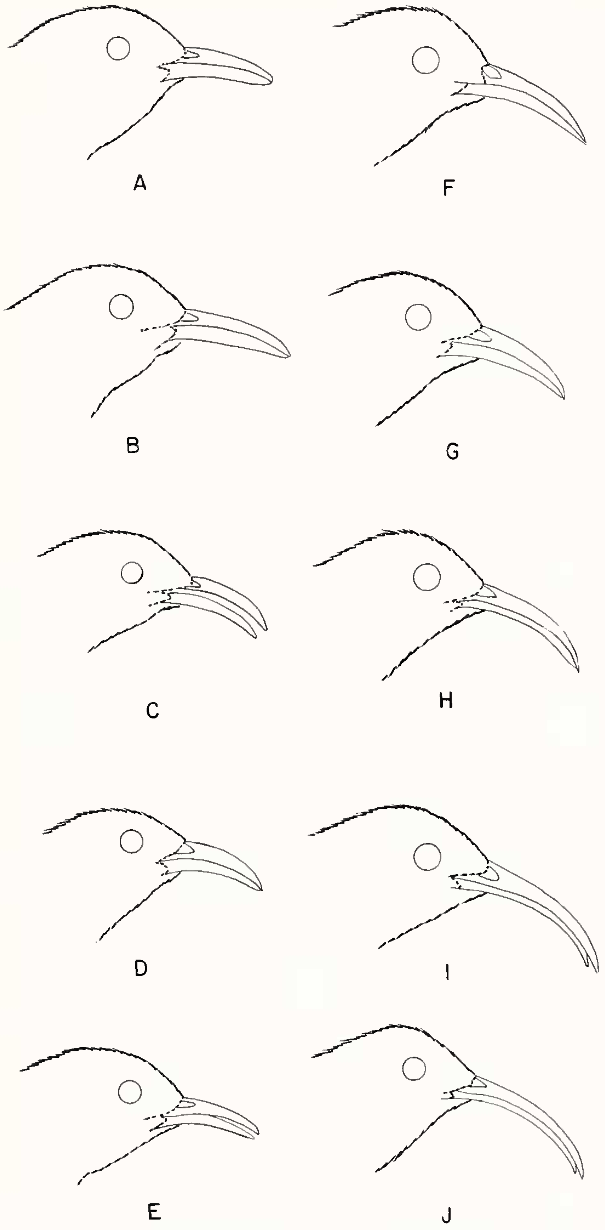


Fig. 20.—Bills of the different species of thrashers (*Toxostoma*) seen in lateral view to show the change in length and in the degree of curvature from the short, straight-billed, *T. rufum* to the heavy curved-billed thrashers. The species are (A) *rufum*, (B) *longirostre*, (C) *guttatum*, (D) *cinereum*, (E) *bendirei*, (F) *ocellatum*, (G) *curvirostre*, (H) *lecontei*, (I) *redivivum*, (J) *dorsale* (taken from Engels, 1940:Fig. 2).

very difficult or impossible to determine the adaptive nature of features in fossils and hence to ascertain actual adaptive change in fossil organisms. It is necessary to turn to observations from Recent organisms to test explanatory models of macroevolutionary change.

The hypothesis to be tested is that macroevolutionary change results from a cumulative summation of chronological small changes along a phyletic lineage and each of these small changes occurs by the known mechanisms of microevolutionary phyletic modification. These vertical phyletic sequences of successive microevolutionary steps can be transformed conceptually to an analogous horizontal series of species in which the difference between adjacent species corresponds to a microevolutionary change and the total difference represents a macroevolutionary modification. The series of horizontal comparisons represents a pseudophylogeny but one analogous to a presumed real phylogeny. The horizontal comparison or sequential species analysis can be undertaken most readily with species-rich genera or groups of closely related genera in which the end forms demonstrate a large difference and which contain enough species to illustrate many stages between the extreme types. The analysis must be a detailed comparison of the descriptive, functional, and ecological morphology of the features involved in the evolutionary change. Unfortunately, these are the types of comparative studies that morphologists have avoided in the past in favor of comparative analyses of large differences in distantly related genera, families, and orders. Relatively few studies are available, which could serve to test the reductionistic model of macroevolution. At this time a request must be made for comparative functional-ecological studies of carefully chosen species-rich genera and genera complexes to obtain observations that would serve to test the reductionistic model. Studies such as those by Webster and Webster (1975, 1977) on the ear of heteromyid mice (kangaroo mice), of Wake and his associates on the plethodontid salamanders of tropical America (see Wake and Lynch, 1976; Lombard and Wake, 1976, 1977) and by Richards and Bock (1973) on the genus *Loxops* (Drepanididae: Aves) are examples of those needed for this testing. I would like to discuss three examples, all from birds, which provide empirical evidence that tests the reductionistic hypothesis.

Engels (1940) reviewed the North American thrashers of the genera *Toxostoma* and *Oreoscoptes* (Passeriformes: Mimidae; these genera are closely related and probably should be considered as congeneric, for example, Mayr and Short, 1970:68). Thrashers are birds of the undergrowth and ground that feed on insects and other small invertebrates, which are found by uncovering the

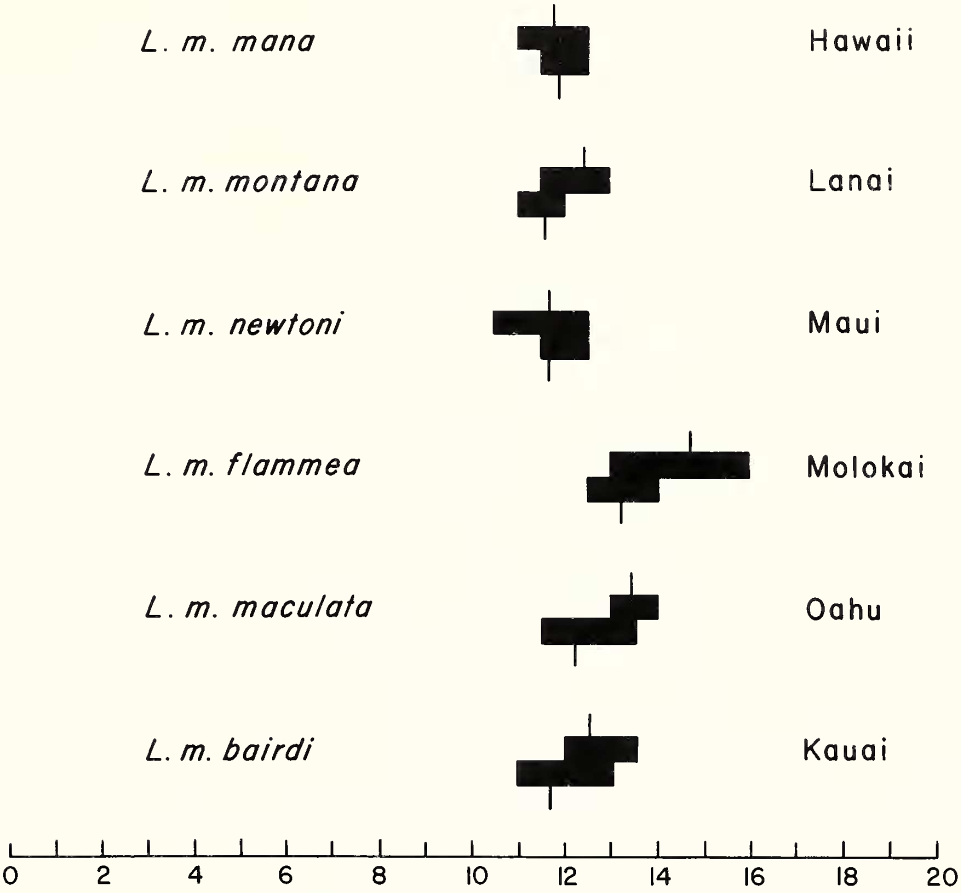


Fig. 21.—Bill length (culmen in mm) of *Loxops maculata* to show pattern of geographic variation; data taken from Amadon (1950). Range is indicated by the sold bar, the mean by the vertical line, males shown by the upper bar and females by the lower (taken from Bock, 1970:Fig. 3).

ground litter with their bills (Fig. 20). Species such as the Sage Thrasher (*Oreoscoptes montanus*, not shown) and the Brown Thrasher (*Toxostoma rufum*) have short, almost straight bills similar to those seen in most other members of the family. A gradual series of increasingly longer and decurved bills are seen in other species of *Toxostoma*. The extreme condition of bill length and curvature is seen in the California Thrasher (*T. redivivum*) and in the Crissal Thrasher (*T. dorsale*) which comprise a superspecies and may be conspecific (Mayr and Short, 1970: 68). Some of the steps in this series are between subspecies or members of a superspecies—for example, the longer and more decurved bill of *longicauda* compared to that of *rufum*.

The curve-billed thrashers use their beak as a pick-ax to dig into the ground and expose their insect prey. The forces involved are considerable judging from the size of the pieces of dirt and the distance they are thrown. Engels describes a suite of morphological changes in the skull and jaw musculature that are associated with the change in bill shape and feeding habits. One of the most obvious is a shift in insertion of a large portion of the M. pterygoideus from a position on the mandible as seen in most passerine birds, including the straight-billed thrashers, to a new position on the base of the braincase in the curve-billed species. The latter is analogous to the structure of the M. pterygoideus seen in the parrots (Psittaciformes). The change in bill structure (and associated internal morphology) and in feeding methods from *Oreoscoptes montanus* to *Toxostoma redivivum* is a major evolutionary change, although at the lower end of the scale, and one which can be clearly demonstrated by a sequential species analysis.

The Hawaiian honeycreepers (Passeriformes:

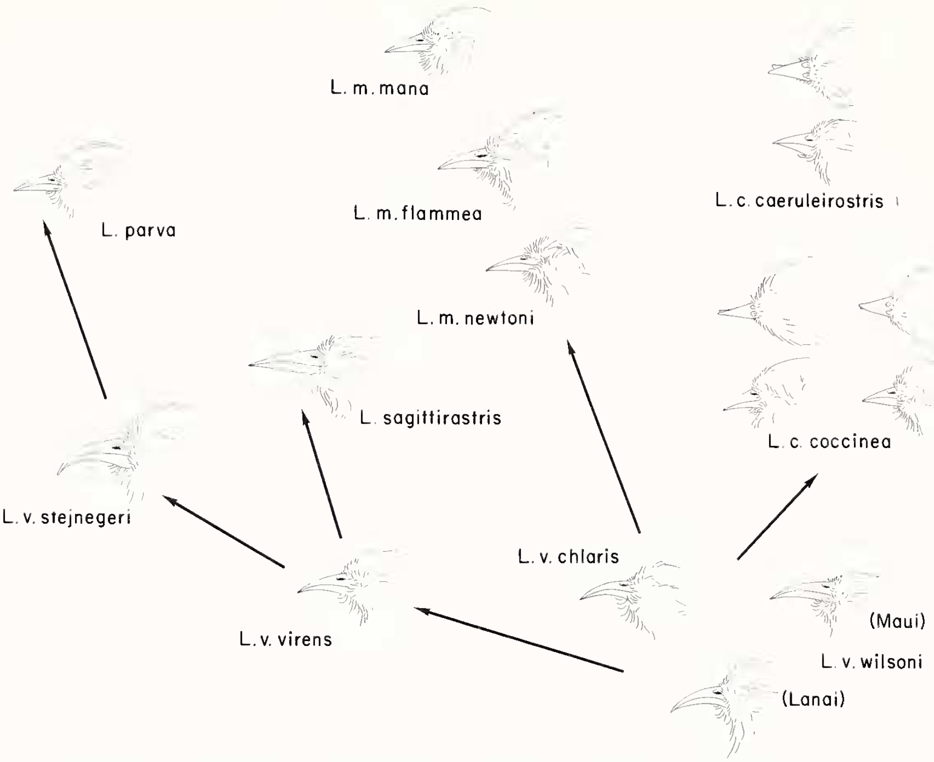


Fig. 22.—Presumed phylogeny of the species of *Loxops* from the ancestral *L. virens*, which stands at the base of the Psittirostrinae. *Loxops* may have evolved from an early member of the Drepanidinae (for example, *Ciridops*) (taken from Bock, 1970:Fig. 6).

Drepanididae) have been a favorite example among evolutionary biologists discussing macroevolution regardless of whether they advocate quantum or reductionistic explanations. They provide an excellent example of a sequential species analysis of a small, but quite diverse adaptive radiation (Bock, 1970) of feeding habits and bill structure. Unfortunately, many of the desired studies of functional and ecological morphology can never be done because of the widespread extinction of species and subspecies and because of the endangered status of a number of the still extant forms.

Several of the widespread species show a pattern of geographic variation from island to island (for example, the *Loxops virens* complex, Fig. 17, and *Loxops maculata*, Fig. 21). Some of the differences between these subspecies are large enough to permit coexistence of the two forms on the same island following invasion should intrinsic isolating mechanisms be fully developed. This had apparently happened in the appearance of *Loxops parva* and *Loxops sagittirostris* at opposite ends of the island chain. A period of exclusionary species interaction and divergence presumably occurred during the neosympatric period. The magnitude of difference observed between the species of the *Loxops virens* complex may be used as a measure of the degree of phyletic evolution on the microlevel in this group. Details of evolutionary change in *Loxops* (Fig. 22) have been presented by Richards and Bock (1973). Most interesting is that a crossed-billed form (*L. coccinea*) had evolved in which the jaw articulation and the jaw muscles have become highly asymmetrical. These species are insect and nectar feeders and include leaf gleaners (*virens*) bark probing creepers (*maculata*), a cross-billed opener of leaf buds and legume pods (*coccinea*), and two deep probing forms (*virens stejnegeri* and *sagittirostris*). Of the last, one is a prober with a decurved bill and the other with a straight bill.

A group of deep bark probers and nectar feeders evolved from a *stejnegeri*-like type, which gave rise to the *Hemignathus* complex (Fig. 23). This group is characterized by an elongated, decurved upper mandible and terminates in the long sickle-billed—*H. obscurus-procerus* superspecies. *Hemignathus wilsoni*, a member of the *lucidus* superspecies, acts like a woodpecker, exposing burrowing insects with

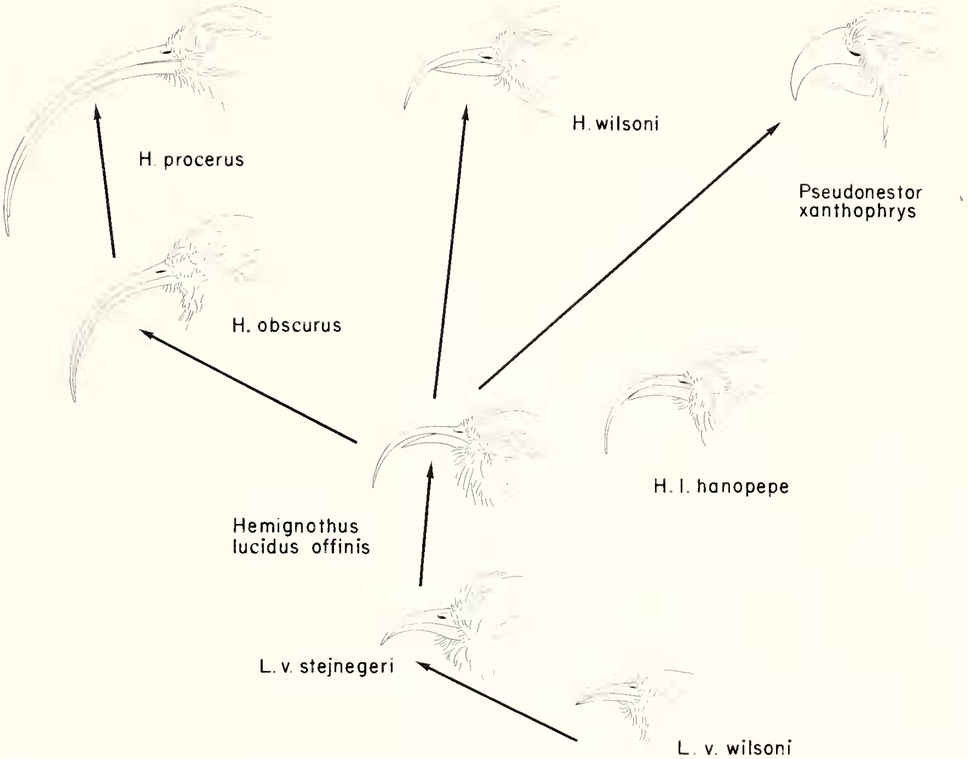


Fig. 23.—Presumed phylogeny of the species of *Hemignathus* and *Pseudonestor* from *L. v. stejnegeri*. The largest-billed members, *L. v. stejnegeri, H. l. hanapepe*, and *H. procerus*, of three successive species are sympatric on Kauai and show the consequences of exclusionary species interaction on this island (taken from Bock, 1970:Fig. 7).

its chisel-like mandible and probing for them with its decurved upper jaw. In another line, *Pseudonestor xanthophrys*, burrowing insects are exposed by crushing twigs with a heavy bill, which still has the decurved overshot upper jaw.

The final radiation of the Psittirostrinae arose from a *Pseudonestor*-like form and gave rise to the *Psittirostra* radiation (Fig. 24). This genus is comprised of a group of insect and plant eating forms. It gave rise to the widespread *Psittirostra psittacea* and its geographic representative *P. cantans* of the leeward islands and a radiation of five species of *Psittirostra*, including *psittacea*, on the island of Hawaii. This is probably the largest number of congeneric species of passerine birds found on a single small oceanic island.

Radiation of the second subfamily, the Drepanidinae, involves somewhat larger steps (Fig. 25), but ones not much greater than seen in the Psittirostrinae. These are all insect and nectar eating species.

Thus, the whole adaptive radiation of the Drepanididae can be explained on the basis of a sequential species analysis with the steps being of the magnitude observed between congeneric (for example, *Loxops*) species. Evolutionary change has been from a finch billed-like form, *Ciridops*, to the sickle-billed *Drepanis* in one subfamily and from the thin-billed leaf gleaner, *Loxops virens*, to a cross-billed *Loxops coccinea*, to the sickle-billed *Hemignathus procerus*, and to the heavy finch-billed *Psittirostra kona* in the other subfamily. The sickle-billed species are as specialized as any passerine birds and *Psittirostra kona* is among the heaviest-billed passeriform finches.

The entire radiation of the Drepanididae, which is surely an excellent example of macroevolution, can be explained completely by sequential species analysis. None of the observed steps in the Psittirostrinae are greater than species differences seen in the primitive genus *Loxops* and those in the Drepanidinae are scarcely greater. Anatomical details have been studied in part of this radiation (for example, *Loxops*, Richards and Bock, 1973). The rest remains to be done.

Perhaps the best support for the reductionistic

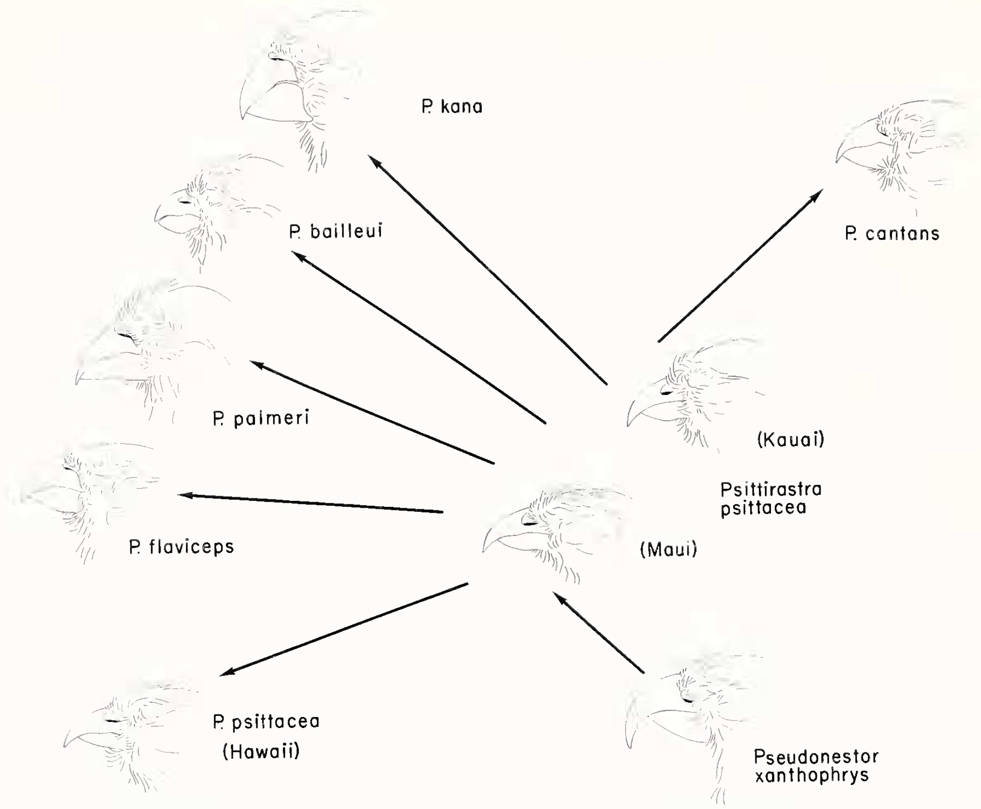


Fig. 24.—Presumed phylogeny of the species of *Psittirostra* from *Pseudonestor*. *Psittirostra contans* is a geographic representative of *P. psittacea* on the leeward islands. The five species, *psittacea*, *flaviceps*, *palmeri*, *bailleui*, and *kona*, are sympatric on Hawaii, but it is not clear whether these are all the result of multiple invasions from Maui or whether some speciated on Hawaii (taken from Bock, 1970:Fig. 8).

model for macroevolutionary change comes from a group of nectar feeding birds, the Australian honeyeaters (Passeriformes: Meliphagidae). Several genera of this family possess a unique articulation of the mandible—the ectethmoid-mandibular articulation in addition to the normal quadrate articulation (Bock and Morioka, 1971). This articulation is best developed in the genus *Melithreptus* (Fig. 26). The mandible has two articulations, one placed far anterior to the other. The ectethmoid articulation serves as a brace for the mandible when the lower jaw is fully adducted. It is analogous to the secondary articulation of the mandible between the internal process of the mandible and base of the braincase seen in many groups of birds (Bock, 1960). Both articulations are excellent analogues of the early stages of the evolution of the mammalian jaw articulation—perhaps the archetype of all major evolutionary changes.

The ectethmoid articulation is well developed and uniform in the seven species of *Melithreptus*. It consists of a distinct process on the mandibular ramus, a fossa in the ventral surface of the ectethmoid, and a definite diarthrosis between these bones. Details of the functional significance and possible biological role of this feature are presented by Bock and Morioka (1971); it appears to be associated with insect feeding with the use of a mucus-coated, sticky tongue. A similar structure is present, but variable in the genus *Manorina*, not closely related to *Melithreptus* within the meliphagids. In this genus, the articulation is absent in *Manorina melanophrys*, is present as a rudiment in *M. melanocephala* and present as a distinct feature, although less well developed than in *Melithreptus*, in *M. flavigula* (Fig. 27) and *M. melanotis*, a pair of sibling species. A rudimentary articulation is present in the New Guinean genus *Ptiloprora* (for example, *P. guisei*) but the distribution of the ectethmoid articulation in this genus is not known with certainty.

Recent observations (Bock, unpublished) fill in

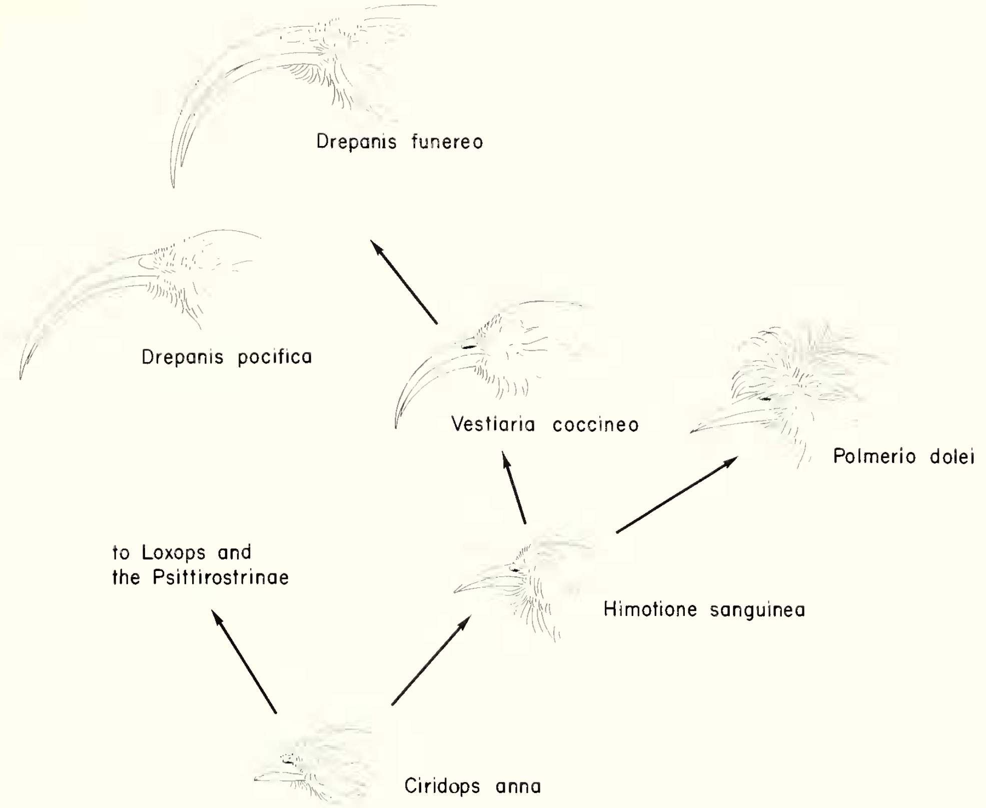


Fig. 25.—Presumed phylogeny of the genera of the Drepanidinae from the ancestral genus *Ciridops*, which may be representative of the founding stock of the Hawaiian honeycreepers (Drepanididae) (taken from Bock, 1970:Fig. 1).

more details of the sequential species analysis illustrating the evolution of the ectethmoid articulation. Two postfledging individuals of *Melithreptus laetior* were examined, which still lack the process suggesting that it arises late in ontogeny. Most interesting is that specimens of local populations of several species of the genus *Meliphaga* (for example, *virescens, keartlandi, fusca, plumula, unicolor, penicillata,* and *flavescens*) showed that the ectethmoid articulation is present as an individual variation in these populations from completely lacking to an extremely poorly developed rudiment to a definite rudiment as well developed as in *Manorina melanocephala.* Some of these species of

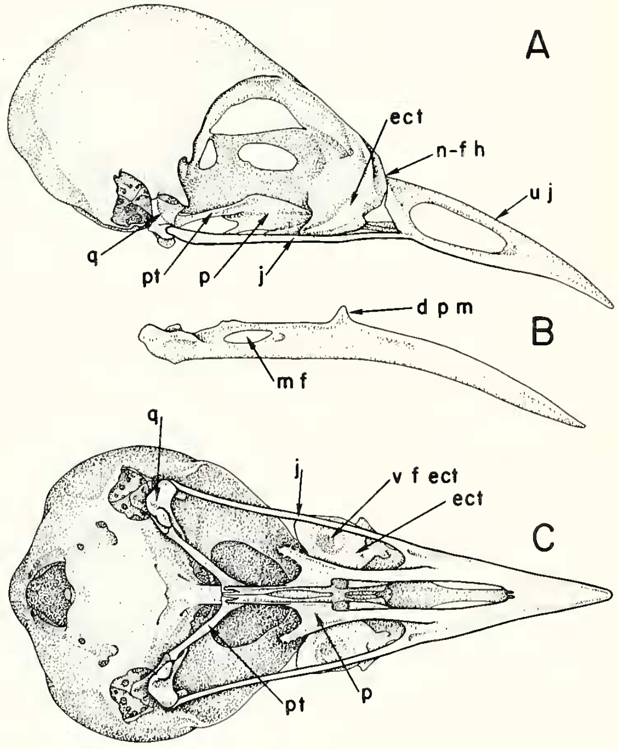


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Fig. 26.—Skull and mandible of *Melithreptus albogularis* (USNM 347,693). (A) Lateral view of the skull. (B) Lateral view of the mandible. (C) Ventral view of the skull. The ecethmoid articulation of the mandible is formed by the dorsal process of the mandible (d p m) with the ventral fossa of the ectethmoid (v f ect) (taken from Bock and Morioka, 1971:Fig. 1).

Meliphaga possessing the ectethmoid articulation as an individual variation are widespread throughout Australia.

Thus, the sequential species analysis of the evolution of the ectethmoid-mandibular articulation in the Meliphagidae shows that this feature is absent in most members of the family, that it exists as an individual variant from absent to a definite rudiment in populations of several species of *Meliphaga*, that it varies from being absent in one species of *Manorina*, a rudiment in another species and well developed in two other species but without any great

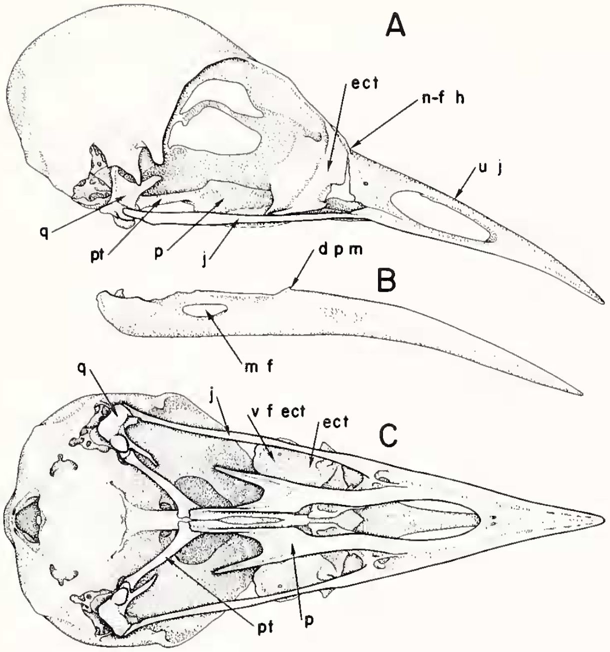

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Fig. 27.—Skull and mandible of *Manorina melanotis* (USNM 345,011). (A) Lateral view of the skull. (B) Lateral view of the mandible. (C) Ventral view of the skull. The ectethmoid articulation of the mandible in this genus is less developed than that seen in *Melithreptus* (taken from Bock and Morioka, 1971:Fig. 5).

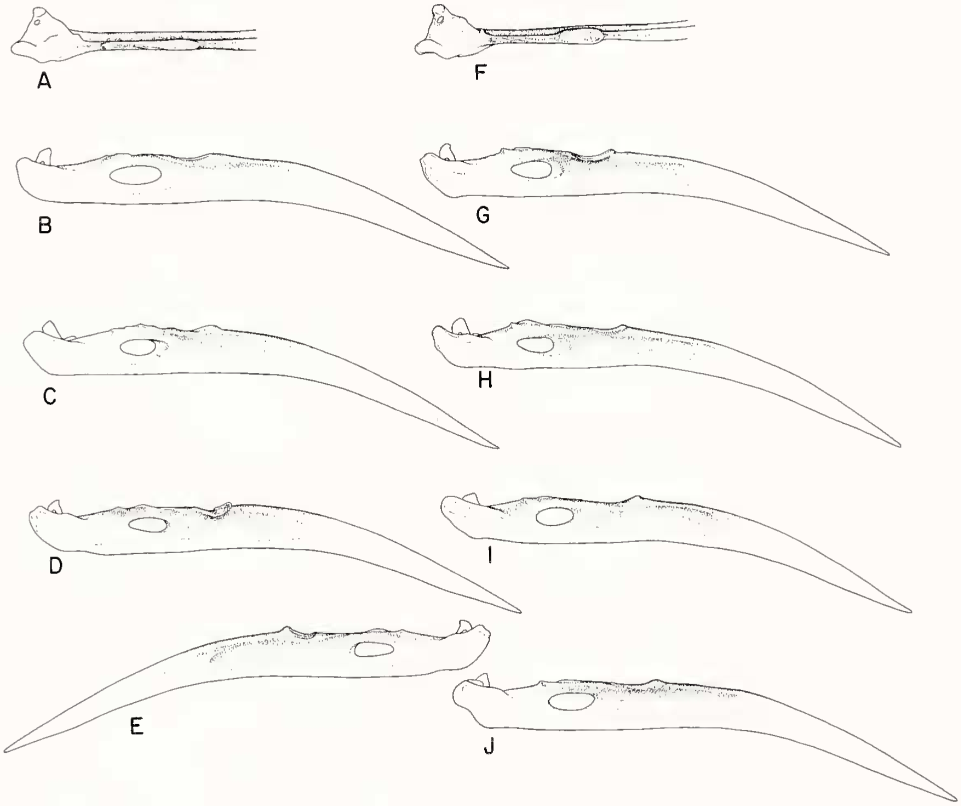

Fig. 28.—Lateral view of the right mandibular rami of a series of seven specimens of *Manorina flavigula* (AMNH uncataloged) to illustrate individual variation in the ectethmoid-mandibular articulation as reflected in the dorsal process of the mandible. Fig. A is the dorsal view of B and Fig. F is the dorsal view of G. Fig. E is the left ramus of the mandible shown in D; the mandible was skewed slightly to the right in this bird. Note the abnormal lip of bone of the dorsal process in Fig. D, which is a result of the bones of the articulation rubbing together incorrectly (taken from Bock and Morioka, 1971:Fig. 8).

variation in any of these species aside from expected individual variation (Fig. 27), and that it is very well developed in all species of *Melithreptus* without any noticable variation between species in spite of the character displacement in feeding habits and bill size of *M. validirostris* and *M. affinis* on Tasmania (Keast, 1968). Moreover, ontogenetic development of this structure is very late in the ontogeny of the individual with no sign of the mandibular process and articulation in adult-sized, fledged young birds.

Thus, the available stages in the horizontal sequential species analysis of the ectethmoid-mandibular articulation provides an analogy to all steps desired in the vertical phyletic evolution of this feature from absent to well developed. All of these stages are taken from species in the same family and some from closely related genera (for example, *Meliphaga* and *Melithreptus*). Many of the morphological details are described with suggestions on the function of this feature (Bock and Morioka, 1971). Only speculations are available on the biological role of this feature and the details of the ecological factors providing selection forces favoring its evolution.

Sufficient variation exists in the structure of the many avian families possessing the secondary (=basitemporal) articulation of the mandible (Bock, 1960) that a similar sequential species analysis could be developed.

In the examples presented, especially for the ectethmoid-mandibular articulation in the Melphagidae, the sequential species analysis provides observations on which to test the hypothesis that macroevolution occurs by successive microevolutionary steps and under the control of the known mechanisms of phyletic microevolutionary change.

CONCLUSIONS

The model of macroevolutionary explanation presented herein argues that all phyletic evolutionary change, small and large, occurs by the action of the same causal evolutionary mechanisms. Macroevolution is simply the consequence of additive microevolutionary change. This explanatory model is silent on rates of these evolutionary changes; presumably, macroevolution occurs at much faster rates than generally supposed. The synthetic or reductionistic model of major evolutionary change is adapted throughout in that selection acts constantly. It can be tested via a conceptual transformation to analogous horizontal sequences which provide suitable pseudophylogenies. These tests can be labelled sequential species analyses.

If macroevolution can be reduced to an additive sequence of microevolutionary steps occurring under the known mechanisms of phyletic evolution, then macroevolution is reduced to microevolution and is fully explained in terms of mechanisms acting on this level. No additional steps, for example, saltation, or additional evolutionary mechanisms are needed for a complete explanation of macroevolution.

Additional studies of sequential species analyses are needed to provide additional tests of the synthetic model of macroevolution and to provide details on the evolution of particular features. These are best done on species-rich genera or groups of closely related genera, and must be comparative studies of descriptive, functional, and ecological morphology. Only after a number of such studies are available from all groups of organisms can we have confidence in the testing of explanatory models of macroevolution.

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CANALIZATION MODEL OF CHROMOSOMAL EVOLUTION

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ABSTRACT

The canalization model implies that the karyotype is a significant aspect in the "adaptive strategy" of an organism and that for each "adaptive zone" there is an optimum karyotype that can be evolved by rearrangements in the karyotype. When an organism invades a new adaptive zone there will be an initial period of karyotypic rearrangement that will continue until the optimum or near optimum karyotype is evolved. After evolution of the optimum karyotype additional evolution will be primarily by genic and morphological mechanisms, not chromosomal rearrangements. An implication of the canalization model is that higher categories are not merely "pigeonholes" that man has created but are real, involving a sequence of orderly events.

INTRODUCTION

The canalization model explains the remarkable difference in patterns of chromosomal variation among different animal groups as a function of the degree to which the optimum karyotype has been achieved for the lineages in an adaptive zone. The taxonomic level at which chromosomal variation occurs will generally be a function of the evolutionary time that a lineage has occupied an adaptive zone. Our model emphasizes the adaptive significance of the karyotype, whereas previous models (White, 1968; Hall, 1973; Wilson et al., 1975) have placed emphasis on chance events that permit chromosomal evolution.

REVIEW OF THE MODELS OF CHROMOSOMAL EVOLUTION IN ANIMALS

Models of Chromosomal Speciation

Cytogenetic studies of Australian flightless morabine grasshoppers by White and colleagues have led to the model of stasipatric speciation (White, 1968, 1974, 1978; White et al., 1967). These animals show a pattern of chromosomal diversity in which virtually every species or race possesses a distinct chromosomal complement, with chromosomal types distributed parapatrically with a slight area of overlap. Hybridization takes place within the zone of overlap, but sterility barriers exist between chromosomally characterized populations. Chance events (genetic drift) or perhaps meiotic drive are responsible for the fixation of chromosomal rearrangements in small, localized demes. These animals have low vagility and a deme may be as small as the number of individuals on a single shrub; therefore, genetic drift is probable. Heterozygotes are thought to be of lower fitness due to meiotic malassortment. If the homozygotes possessing the new arrangement are more fit than the heterozygotes and the parental homozygotes, it can spread into previously unoccupied territory and/or into the territory of the parental population (displacing the parental type) until an equilibrium is reached, with a small zone of overlap at the border of the two populations.

Although White (1968, 1974, 1978) believed the process of stasipatric speciation could take place at the periphery or well within the distributional range of a species, other workers contend that the establishment of chromosomal rearrangements will be restricted to small peripheral populations (Bush, 1975; Key, 1968; Patton, 1969).

Bush (1975) has divided models of speciation into four basic kinds, with chromosomal evolution associated with two—parapatric speciation, which is essentially the stasipatric model of White as ammended by subsequent workers (Bush, 1975; Key, 1968; Patton, 1969), and speciation by the founder effect.

Hall (1973) has proposed a "cascading chromosomal speciation" model that is similar to the stasipatric model of White. The cascading model is based on chromosomal variation in a wood crevice inhabiting species of iguanid lizard (*Sceloporus grammicus*) (Hall and Selander, 1973). Like the stasipatric model, Hall envisions chromosomal rearrangements becoming fixed by genetic drift in small, inbred demes, and subsequent range expansion due to competitive advantage. The cascading model differs from other models in that Hall envisions a linear pattern to chromosomal speciation, an apparent rapid nature of chromosomal speciation, and alternative mechanics of contact hybridization.

The above mentioned models possess a common theme. Chromosomal rearrangements act as cytogenetic isolating mechansims that serve to maintain species integrity, because of negative heterosis. Chromosomal rearrangements come to fixation by chance events in small, inbred demes. Thus, animals that speciate in this way are characterized by low vagility or social structure that promotes inbreeding (Arnason, 1972; Bush, 1975). Natural selection plays a positive role in the process only after a population of the new homozygote is established. Selection accounts for subsequent expansion of the range of the new chromosomal type, although none of the above models state precisely why or how the chromosomal alteration gives new species an adaptive advantage.

Significance of Chromosomal Variation

A series of papers by A. C. Wilson and colleagues (Wilson, 1976; Wilson et al., 1974*a*, 1974*b*, 1975; Maxson and Wilson, 1975; Prager and Wilson, 1975) have developed hypotheses to explain the role that chromosomal changes have played in the evolution of organisms. Based on studies of placental mammals and frogs (Wilson et al., 1974*a*, 1974*b*; Maxson and Wilson, 1975) and birds (Prager and Wilson, 1975), they conclude that organismal (morphological) evolution is correlated with chromosomal but not genic evolution. Their reasoning is as follows. Frogs have experienced a slow rate of morphological change, are an old group (150 million years) with over 3,000 species, but consist of only a single order. Placental mammals are a younger group (75 million years) of about 4,600 species and 16–20 orders, which have evolved rapidly at the organismal level. Both groups have evolved at an equal rate on the genic level; however, based on diploid and fundamental number, mammals have experienced considerably more rapid chromosomal evolution. Birds follow the same pattern as frogs (Prager and Wilson, 1975).

Their explanation for this phenomenon is that chromosomal changes are a source of genetic regulatory change. The evidence for this is largely indirect. It is known from genetics of microorganisms that gene regulation can play an important role in the adaptive process (Wilson, 1976). Chromosomal rearrangements can also effect the regulation of structural genes by placing them next to a different set of gene loci, the "position effect" known in *Drosophila* (Bahn, 1971). Wilson and colleagues point out that frogs (Wilson et al., 1974*a*) and birds (Prager and Wilson, 1975) have the ability to form hybrids between species that are considerably more genically distinct than do placental mammals, which they interpret as meaning that chromosomal changes alter the regulatory systems of genes which result in the inability of mammals (which have extensive chromosomal evolution) to form interspecific hybrids. They conclude that genetic regulatory changes are a primary source of the more rapid organismal evolution of mammals.

Wilson et al. (1975) and Bush (1975) suggest that placental mammals have achieved a high degree of inbreeding and small population size due to their social structure. The small population size facilitates fixation of chromosomal rearrangements that are thought to be deleterious in the heterozygous state. Thus, drift is again ascribed as a requisite mechanism for evolution of new chromosomal complements. Frogs, and other lower vertebrates, are presumed to have a lower rate of karyotypic change than placental mammals because they do not have the complex social behavior that produces small deme size (see also Bush et al., 1977).

PATTERNS OF CHROMOSOMAL VARIATION IN DIVERSE GROUPS OF VERTEBRATES

Patterns of chromosomal variation within orders of vertebrates (especially turtles, Order Testudines, and bats, Order Chiroptera) have led us to question the above models as the best explanation of patterns of chromosomal variation in vertebrates. All orders discussed below encompass extensive chromosomal diversity, but the taxonomic levels that exhibit chromosomal stability vary between orders.

Table 1.—*The families and subfamilies of cryptodiran turtles with geological ages, number of species, and chromosomal diversity.*

Group	No. species	Age	$2n$ (followed by no. of known species)
Kinosternidae		Oligocene	
Kinosterninae	19		56 (12), Unknown (7)
Staurotypinae	3		54 (3)
Carettochelyidae	1	Eocene	Unknown (1)
Trionychidae		Cretaceous	
Trionychinae	18		52–54 (1), 64 (1), 66 (6), Unknown (10)
Cyclanorbinae	5		66 (1), Unknown (4)
Dermatemyidae	1	Cretaceous	Unknown (1)
Dermochelidae	1	Eocene	Unknown (1)
Cheloniidae	6	Cretaceous	56 (2), 58 (1), Unknown (3)
Chelydridae		Paleocene	
Chelydrinae	3		52 (3)
Platysterninae	1		54 (1)
Emydidae		Paleocene	
Emydinae	37		50 (22), Unknown (15)
Batagurinae	47		50 (2), 52 (12), 56 (1), Unknown (32)
Testudinidae	38	Eocene	52 (6), Unknown (32)
Total	186		

The factor that seems to be correlated with this pattern of stability is the geological age of the group—older groups exhibit chromosomal stability at higher taxonomic levels than is characteristic of younger groups. Some data which support these conclusions follow.

Order Testudines

Chromosomal evolution.—The S-necked turtles, Infraorder Cryptodira of Gaffney (1975), which encompass some 200 species and 10 families, are distributed on all of the major land masses, except Antarctica (albeit marine turtles are the only representatives in Australia), and even on many of the oceanic islands (for example, the tortoises of the Galapagos and Aldabra islands).

Examination of the geological age and the available diploid numbers of the families and subfamilies of Cryptodira (Table 1) reveals karyotypic stability within each family or subfamily. For example, each of the two subfamilies of Kinosternidae is characterized by a single diploid number (Staurotypinae $2n = 54$, Kinosterinae $2n = 56$), the subfamily Emydinae are all $2n = 50$, nearly all trionychids so far studied are $2n = 66$, all testudinids studied are $2n = 52$.

Conservatism in diploid numbers is seen in standard and banded karyotypes. G-band studies of the emydine turtles revealed no variation in karyotypes of the species studied (Bickham and Baker, 1976*a*, 1976*b*). Fig. 1 shows G-banded karyotypes of three morphologically diverse genera of emydines where no karyotypic differences were detected. Karyotypes of the emydid subfamily Batagurinae are more variable ($2n = 50$, 52, 56) than those of the emydines. However, in almost all species the diploid number is 52 with two species being reported as 50, and one species, 56 (this latter species, *Rhinoclemys punctularia*, differs from a $2n = 52$ congener by the addition of some heterochromatic microchromosomes). Comparisons of banded karyotypes between the two subfamilies indicate a high degree of homology (Bickham and Baker, 1976*a*) in that all macrochromosomes of the emydines can be identified in such batagurines as *Sacalia*. *Rhinoclemys* has fewer macrochromosomes and a higher number of microchromosomes, but the macrochromosomes present can be identified in emydines and other batagurines. Banding data for chelydrids, emydids, and kinosternids were compared by Sites et al. (1979) and nearly all of the macrochromosomes appear to have homologues in each of the three families although there appears to be some differences between each. In all testudinids (tortoises) reported in the literature, the diploid number is 52 (Bickham and Baker, 1976*a*, 1976*b*; Stock, 1972), and the karyotypes reported for certain species of *Geochelone* are indistinguishable from those of some $2n = 52$ batagurines (Bickham and Baker, 1976*a*).

The family Kinosternidae is a fairly abundant group restricted to the New World. A single karyotype is known for the entire subfamily Kinosterinae (two genera, *ca.* 20 species, Table 1). The subfamily Staurotypinae is characterized by a different diploid number with several structural karyotypic differences, but all staurotypines have a virtually identical karyotype (Bull et al., 1974). Many of the kinosternid macrochromosomes have homologues in emydids and chelydrids. Fig. 2 is a comparison of the banded karyotypes of a kinosternine and an

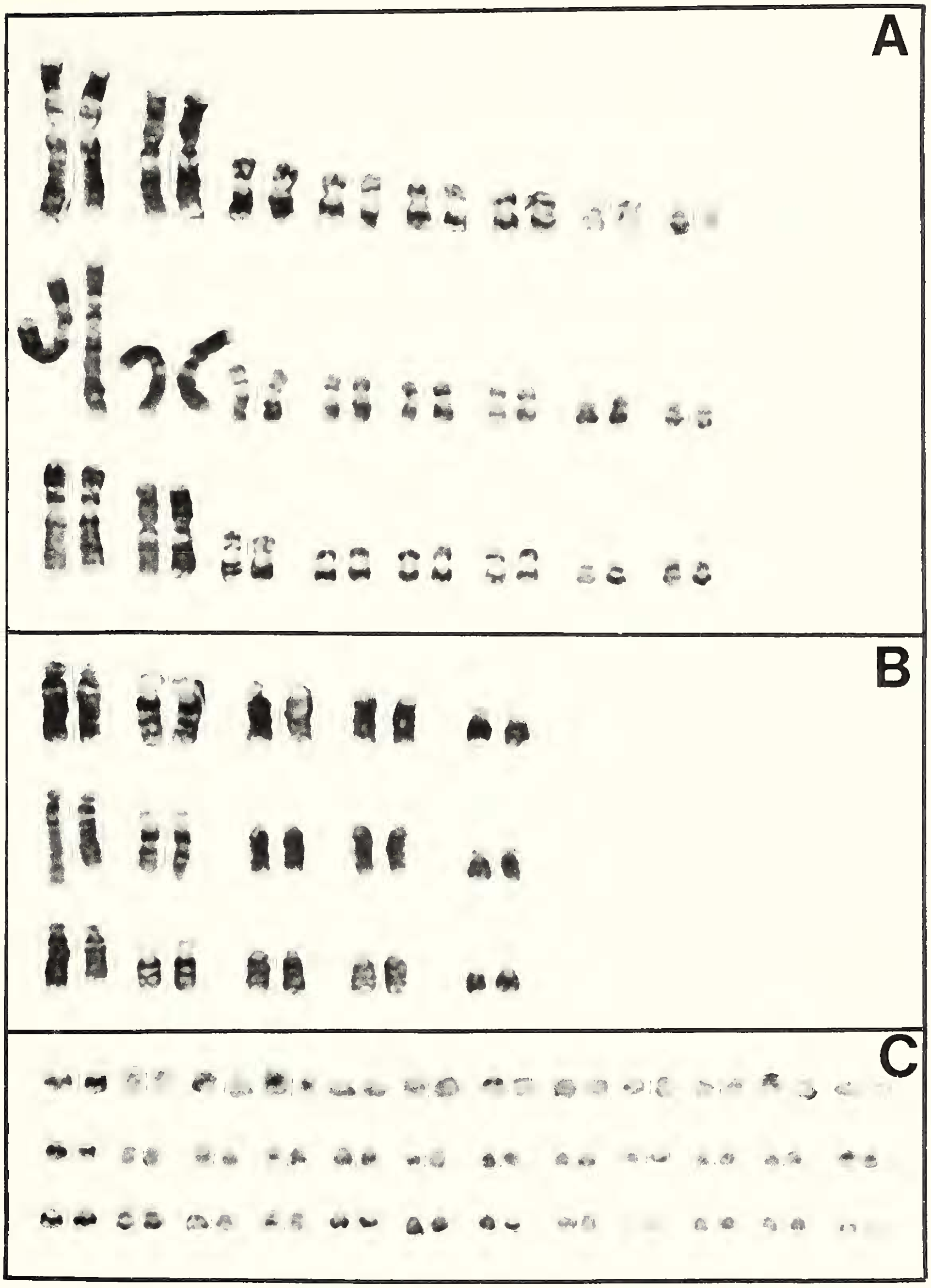

Fig. 1.—G-band comparison of three morphologically diverse genera of emydine turtles to demonstrate karyotypic stability within higher categories of turtles. The chromosomes are arranged into three groups (A, B, C) according to Bickham (1975). The top row in each group is from *Chrysemys decorata*, $2n = 50$; the middle row in each group is from *Graptemys pseudogeographica*, $2n = 50$; the bottom row in each group is from *Terapene carolina*, $2n = 50$. No differences in banding pattern can be detected in the macrochromosomes (groups A and B); the microchromosomes (group C) cannot be reliably identified, but all three species possess 12 pairs.

emydine. Although most of the macrochromosomes appear to be homologous, there are several that have undergone rearrangements since divergence from a common ancestor.

The family Trionychidae is both morphologically and chromosomally quite distinct from the families discussed above. They are characterized by a $2n = 66$ karyotype except for one known exception (Gorman, 1973).

Morphological evolution.—Turtles probably

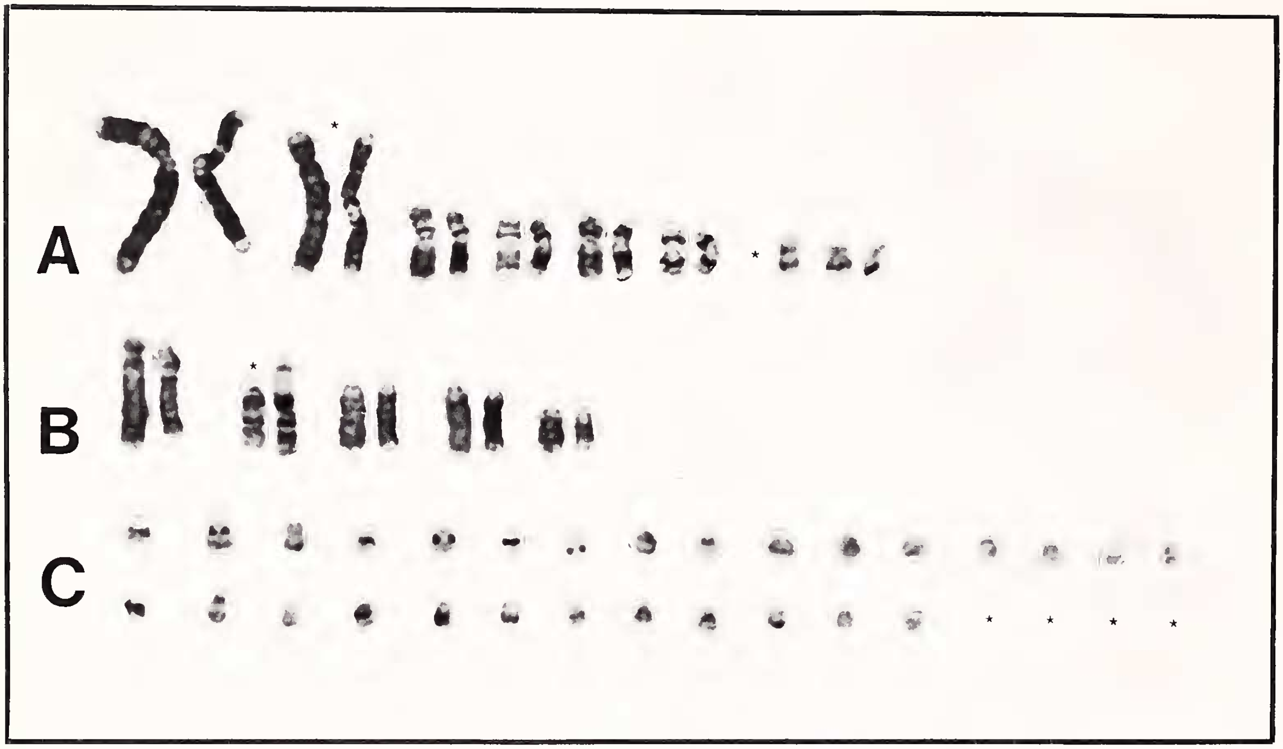

Fig. 2.—G-band comparison of a kinosternid and an emydid turtle to demonstrate the degree of chromosomal homology between higher categories of turtles. In groups A and B the right member of each pair is from *Chrysemys concinna* (Emydidae) $2n = 50$, and the left member is from *Sternotherus minor* (Kinosternidae) $2n = 56$. The microchromosomes (group C) cannot be reliably identified, the top row is from *Sternotherus* and the bottom row is from *Chrysemys*. An asterisk indicates an identifiable chromosomal difference between the two species. The second pair in group A differs in centromere position; the seventh pair in group A differs by the absence of this chromosome from the *Sternotherus* complement. The second pair in Group B is acrocentric in *Sternotherus* and subtelocentric in *Chrysemys*. There are four more pairs of group C microchromosomes in *Sternotherus* than there are in *Chrysemys*.

originated in the lower Triassic and had already undergone a long period of evolution before the two modern groups (pleurodires and cryptodires) first appear in the Jurassic. Cryptodiran families are relatively old (Table 1), ranging from the Dermatemyidae (no chromosomal data) and the Trionychidae from the Cretaceous, to the Kinosternidae from the Oligocene. No family is of a relatively young age.

Although karyotypic data are lacking for over half of the species and even some families of cryptodires, there is a definite pattern to the variation already documented. Higher categories (families and subfamilies) are, for the most part, characterized by a single, almost unvarying karyotype, but each group is distinct from the others. At the lower levels of classification (genus and species) there is almost no variation, which indicates that recent turtles have undergone speciation in the absence of chromosomal rearrangements. However, the differences seen between higher categories indicate that during the origin and establishment of modern families and subfamilies there was a period of chromosomal evolution. This has been followed by morphological diversification within the larger families that was not accompanied by significant amounts of chromosomal evolution. An example of morphological diversification with the absence of chromosome diversity is found in the diverse genera *Graptemys*, *Chrysemys*, *Terrapene*, and others in the Emydinae that all have identical karyotypes (Fig. 1). The same pattern is present in other families or subfamilies of turtles.

Order Chiroptera

Our discussion will be limited to the Suborder Microchiroptera, which is nearly worldwide in distribution and encompasses 16 extant families and more than 720 living species. Reviews of bat cytosystematics (Baker, 1970; Capanna and Civitelli,

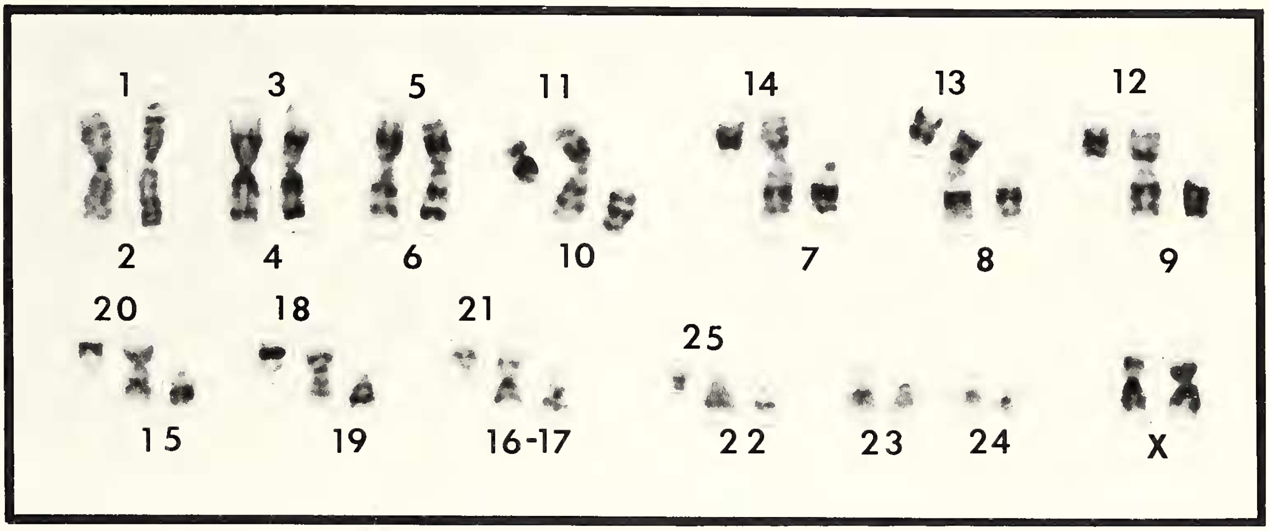

Fig. 3.—G-band comparison of two morphologically distinct genera of vespertilionid bats to demonstrate the degree of chromosomal homology within higher categories of bats. Chromosomal arms are identified and numbered according to Bickham (1979*b*). The left member of the first three pairs is from *Lasiurus borealis* $2n = 28$, the right member is from *Myotis sodalis* $2n = 44$. In the next eight triplets, the biarmed element is from *Lasiurus* and the acrocentric homologues are from *Myotis*. In pairs 23, 24, and X the left member is from *Lasiurus*. Centric fusions account for nearly all of the variation between these species.

1970; Matthey, 1973) are somewhat out of date, but they allow an assessment of the patterns of chromosomal variation in bat evolution.

Vespertilionid chromosomal evolution.—The largest family of bats (287 species, 33 genera, and six subfamilies) has been studied reasonably well for standard and banded karyotypes (Ando et al., 1977; Baker, 1970; Bickham, 1979*a*; Capanna and Civitelli, 1970). Most genera of vespertilionids are characterized by a single diploid number and karyotype; for example, genus *Myotis* (Bickham, 1979*b*) where all species studied possess virtually identical karyotypes with a $2n = 44$. Members of *Eptesicus* studied have $2n = 50$, except one African species (Peterson and Nagorsen, 1975). Members of *Lasiurus* have $2n = 28$ except *L. intermedius* with $2n = 26$. Members of the genus *Plecotus* all have $2n = 32$, as does the closely related genus *Barbastella*.

The two genera of vespertilionids that differ from this pattern of chromosomal stability are *Rhogeesa* ($2n = 30$–44) and *Pipistrellus* ($2n = 26$–44). The differences between genera and within the variable genera can be explained primarily by Robertsonian mechanisms (centric fusion and fission of whole arms), whereas non-Robertsonian rearrangements (such as inversions and reciprocal translocations) are rare (Bickham, 1979*a*; Bickham and Baker, 1977). Thus, the general pattern of chromosomal variation seen within vespertilionids is one of conservatism below the generic level but with nearly all genera differing from one another by Robertsonian variation. Because Robertsonian mechanisms are involved, the basic chromosomal banding pattern is conserved in vespertilionids to the extent that the chromosomal banding sequence of all segments can be identified in such disparate forms as *Myotis* ($2n = 44$) and *Lasiurus* ($2n = 28$) (see Fig. 3).

Phyllostomatid chromosomal evolution.—This family shows a pattern of variation similar to that of the Vespertilionidae. Recent studies (Baker, 1978; Gardner, 1977) reveal that a few genera (that is, *Macrotus*, *Uroderma*, *Vampyressa*, and *Micronycteris*) show interspecific or intraspecific variation. Except for these few genera, most of the chromosomal variation in phyllostomatids is at the generic level or higher. Banding studies demonstrate that in most cases homologous elements can be demonstrated among all genera (Baker and Bass, 1979; Baker et al., 1979; Patton and Baker, 1979). With some notable exceptions, intergeneric variation is due to Robertsonian change and G-banding patterns are conserved.

Although diverse genera within the families Vespertilionidae and Phyllostomatidae show considerable banding homology, comparisons made between species from different families may show little banding homology. Fig. 4 shows a banding

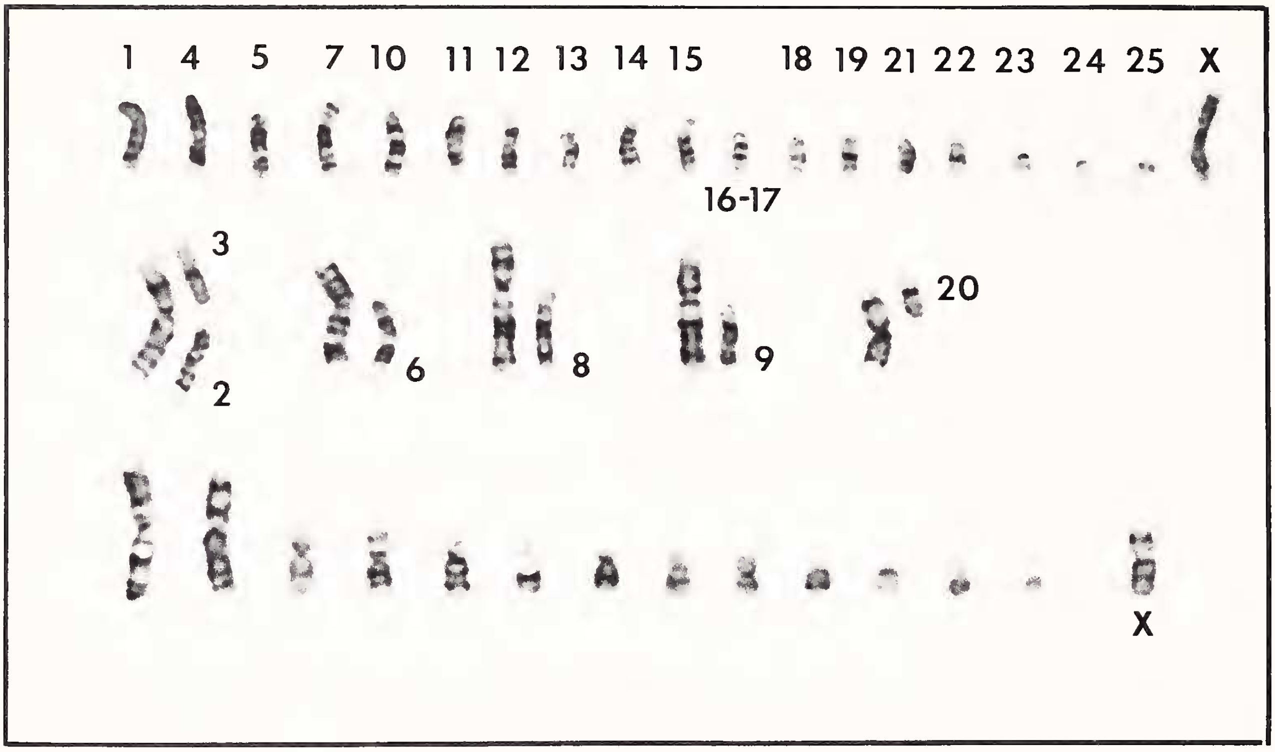

Fig. 4.—G-band comparison of a mormoopid and a vespertilionid bat to show the slight amount of chromosomal homology characteristic of interfamilial comparisons of bats. The top row are chromosomes from *Eptesicus fuscus* (Vespertilionidae) $2n = 50$ that do not show identifiable homologues in *Mormoops blainvilli* (Mormoopidae) $2n = 38$. The middle row are homologous elements identifiable between the two species, the acrocentrics are from *Eptesicus* and the biarmed chromosomes are from *Mormoops*. The bottom row are unpaired elements from *Mormoops*. Of the 24 autosomal arms of *Eptesicus*, only six can be identified in *Mormoops*, a considerable number of non-Robertsonian changes have taken place since the divergence of these two species. The *Eptesicus* chromosomes are numbered according to Bickham (1979*b*).

Table 2.—*The families of microchiropteran bats, with number of species and geological ages.*

Family	No. extant species	Age
Rhinopomatidae	2	Recent
Emballonuridae	44	Upper Eocene–Lower Oligocene
Noctilionidae	2	Recent
Nycteridae	13	Recent
Megadermatidae	5	Upper Eocene–Lower Oligocene
Rhinolophidae	128	Middle Eocene
Phyllostomatidae	120	Miocene
Mormoopidae	8	Pleistocene
Natalidae	4	Pleistocene
Furipteridae	2	Recent
Thyropteridae	2	Recent
Myzopodidae	1	Recent
Vespertilionidae	283	Upper Eocene
Mystacinidae	1	Recent
Molossidae	82	Upper Oligocene
Total	697	

comparison between a vespertilionid and mormoopid. Only six autosomal arms can be identified between the two. Thus, the kinds of rearrangements involved in separating these two families include a sufficient number of non-Robertsonian changes to make arm identification impossible. Few interfamilial homologies can be identified among the families Vespertilionidae, Molossidae, and Phyllostomatidae. An exception is seen in comparisons of Phyllostomatidae, Noctilionidae, and Mormoopidae (Baker and Bass, 1979; Baker et al., 1979; Patton and Baker, 1979). These three families are related at the superfamily level and the mormoopids and phyllostomatids were considered confamilial in the past.

To summarize the general pattern of chromosomal variation in bats, there is a consistent stability below the generic level, considerable variation among genera or closely related groups of genera, remarkable conservatism of banding patterns within

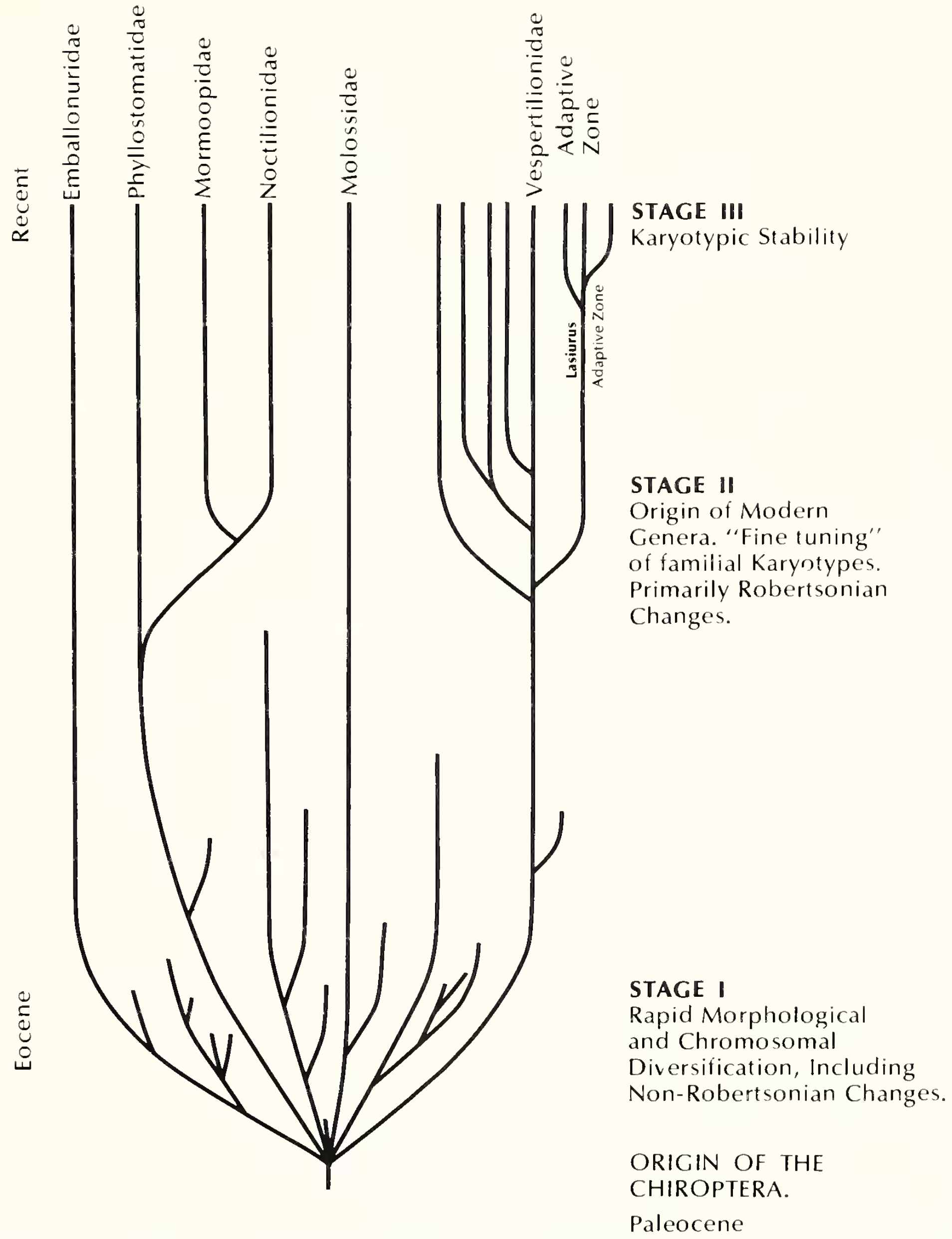
Recent
Emballonuridae
Phyllostomatidae
Mormoopidae
Noctilionidae
Molossidae
Vespertilionidae
Adaptive Zone
Lasiurus
Adaptive Zone
Eocene
STAGE III
Karyotypic Stability
STAGE II
Origin of Modern Genera. "Fine tuning" of familial Karyotypes. Primarily Robertsonian Changes.
STAGE I
Rapid Morphological and Chromosomal Diversification, Including Non-Robertsonian Changes.
ORIGIN OF THE CHIROPTERA.
Paleocene

Fig. 5.—Schematic representation of the events characteristic of the canalization model as related to some bat families.

families, but very little homology between many families. It appears that Robertsonian mechanisms are most important within families (that is, have been used to rearrange the karyotypes characteristic of different genera) but non-Robertsonian changes are more important in explaining the karyotypic differences between such families as Phyllostomatidae, Molossidae, and Vespertilionidae.

Morphological evolution.—Bats are thought to have evolved from an arboreal insectivore sometime during the Paleocene (Fig. 5). The fossil record is not as good as for most other mammals, and there are no fossils of any transitional forms. An early Eocene bat, *Icaronycteris index* from Wyoming, is already morphologically highly advanced and, for the most part, a typical bat. Thus, bats apparently underwent a period of rapid development during the Paleocene. By the end of the Eocene many of the modern families (Emballonuridae, Megadermatidae, Rhinolophidae, and Vespertilionidae) were already present (Table 2). Many of the modern genera are quite old. *Myotis*, for example, first appeared in the Oligocene. It is apparent that bats are an old group, relative to other mammals, but their fossil records are spotty. Thus, values listed in Table 2 may well be an underestimate of the age of most families.

Table 3.—*The families of rodents, with number of species and geological ages.*

Family	No. extant species	Age
Aplodontidae	1	Upper Eocene
Sciuridae	261	Upper Eocene or Lower Oligocene
Octodontidae	8	Lower Oligocene
Echimyidae	43	Lower Oligocene
Ctenomyidae	26	Upper Pliocene
Abrocomidae	2	Middle Pliocene
Capromyidae	11	Middle Pliocene
Chinchillidae	6	Lower Oligocene
Dasyproctidae	11	Lower Oligocene
Dinomyidae	1	Lower Miocene
Caviidae	12	Upper Miocene
Hydrochoeridae	2	Lower Pliocene
Erithozontidae	8	Lower Oligocene
Cricetidae	567	Lower Oligocene
Muridae	457	Lower Miocene
Dipodidae	27	Upper Oligocene
Zapodidae	11	Upper Oligocene
Geomyidae	40	Upper Eocene
Heteromyidae	75	Lower Oligocene
Gliridae	23	Upper Eocene
Spalacidae	3	Lower Pliocene
Rhizomyidae	18	Middle Oligocene
Castoridae	2	Lower Oligocene
Thryonomyidae	6	Lower Miocene
Bathyergidae	22	Pleistocene
Hystricidae	15	Oligocene
Ctenodactylidae	8	Upper Oligocene
Anomaluridae	12	Lower Miocene
Pedetidae	2	Lower Miocene
Total	1,681	

Order Rodentia

Chromosomal evolution.—Rodents have received a major portion of the attention of cytogeneticists compared to other vertebrate orders. Rodents contrast with bats and turtles in the nature of their karyological diversity. Such genera as *Dipodomys, Perognathus, Peromyscus, Sigmodon, Oryzomys, Thomomys, Geomys, Spalax,* and others are all karyotypically diverse and interspecific (and a high level of intraspecific) chromosomal diversity is the rule rather than the exception. Mascarello et al. (1974) demonstrated that comparisons of banded chromosomes between the murid-crecetid complex revealed a considerable homology between distantly related genera. Comparisons made between the more distantly related families Cricetidae and Heteromyidae revealed no homology. This is similar to the pattern of variation at the generic and familial levels in bats.

Morphological evolution.—Rodents originated in the Paleocene (Romer, 1966), as did bats; however, most rodent families are younger than most modern bat families (disregarding those without a fossil record). For example, the large and diverse families Cricetidae and Heteromyidae appear in the lower Oligocene (Table 3), but the Muridae appear in the lower Miocene. Although some of the modern rodent families are as old as bat families (Eocene-Early Oligocene) (Table 3), there has been a considerable diversification and a relatively recent origin (Upper Oligocene, Miocene, Pliocene, and even Pleistocene) for many rodent families. Also, rodents seem to fossilize much better than bats and their fossil records are probably a better estimate of their actual ages than are those of bat families. We conclude that the primary diversification of rodents has been more recent than that of bats and turtles.

THE CANALIZATION MODEL

A major tenet of the canalization model is that the karyotype contributes significantly to the fitness of the individual and that, for a given set of biological parameters faced by an evolving lineage, there is an optimal karyotype. The karyotype, which is a product of selection for arrangement of genes (supergenes, position effect), size and number of linkage groups, centromere position, regulatory function, and others, is an important means of achieving an adaptive phenotype. The model predicts that the role of chromosomal evolution is most rapid immediately after a lineage breaks into a new adaptive zone and the rate becomes slower through time. The model further predicts that chromosomal stability would characterize lineages that have evolved the optimum karyotype for their adaptive zone (with chromosomal fitness maximized, additional evolution would be by means other than chromosomal). The taxonomic level at which chromosomal stability occurs would be a function of the amount of morphological divergence that had occurred since a lineage had attained its optimal karyotype. In most cases, this would strongly correlate with the amount of time since a lineage had attained its optimum karyotype.

The origin of any higher category is ultimately an ancestral population that achieves an evolutionary breakthrough into a new adaptive zone; the broader the zone, the higher the category (Bock, 1965; Schaeffer, 1976; Mayr, 1963; Simpson, 1959). Problems concerning the origin and development, and the biological reality of higher categories have been addressed by numerous authors (for example, Schaeffer, 1976); however, little discussion has been given to the role of chromosomal evolution in regard to the development of higher categories.

Once the breakthrough is made and the adaptive morphological complex is more or less functional (such as flight in bats and protective shell in turtles), the progenitor will spread and diversify into lineages which become adapted to subdivisions of the zone. This whole process may be relatively rapid, which may explain why there usually are few fossil intermediates between orders (see Bock, 1965 for more thorough discussion of this process). We have divided the process of evolution into a new adaptive zone into three stages (Fig. 5).

Stage I

This stage is characterized by rapid diversification, with members of the radiating group poorly adapted to the new zone either morphologically or karyotypically. Each lineage will generally be characterized by chromosomal changes. Data from bats and turtles suggest that karyotypic evolution in Stage I is often non-Robertsonian rearrangements that serve to radically alter the arrangement of genes and the nature of linkage groups and, hence, the banding patterns of the chromosomes. There is evidence to suggest that chromosomal rearrangements serve to alter genetic regulatory systems and, thus, serve to enhance rapid evolution (Wilson, 1976; Wilson et al., 1974*a*, 1974*b*). During this time there is rapid development of independent lineages within the order, aided by the effects of different gene arrangements. Some of the successful lineages evolve highly adaptive gene arrangements.

Lineages within the order that have evolved a highly adaptive karyotype invade new and distinct subzones of the ordinal level adaptive zones. These subzones are familial level zones and the lineages that achieve these breakthroughs diversify, but in a more restrictive context than when the ordinal zone was invaded.

Stage II

Chromosomal evolution is now much more restricted (canalized). At this stage lineages are characterized by gene arrangements that are reasonably well adapted and, at this point, non-Robertsonian rearrangements (inversions and others) are generally selected against because they serve to break up adaptive linkage groups. Diversification takes place within the family zone and chromosomal evolution proceeds primarily by Robertsonian fusions and fissions, or by non-Robertsonian mechanisms, such as telomere-telomere fusions, that do not markedly alter the gene arrangements and banding patterns. As a result, homologies can be determined between even very ancient and morphologically very distinct genera within a family. This seems to be generally true in reptiles and mammals. We hypothesize that most chromosomal changes that do become established are adaptive, but seem to be a "fine tuning" of the generally adaptive familial karyotype.

Stage III

When the karyotype is essentially optimum, nearly all karyotypic mutations are nonadaptive and the lineage becomes karyotypically "stable." Further evolution and speciation in such a lineage proceeds primarily by means that are not associated with karyotypic change. Thus, in our example in Fig. 5, *Lasiurus* species have virtually identical karyotypes, but are morphologically distinct. As time goes on, further morphological differentiation may become established between the lineages within the *Lasiurus* generic adaptive zone, but few, if any, karyotypic alterations will be selected for. As a result of canalization, the karyotype of *Lasiurus* is adaptive and stable. We envision that as the lineage becomes older, this generic group might evolve sufficient morphological differences to justify it being divided into units with a higher taxonomic rank, as is the case in the karyotypically stable Phyllonycterinae or the Emydinae. Various families of lower vertebrates seem to be karyotypically stable and at the same time quite old (Trionychidae and Emydidae, for example).

Once lineages develop more "optimum" karyotypes, and some lineages become extinct, new radiations of surviving lines will be accompanied by less chromosomal diversity. This, in part, explains why there are often no species with intermediate karyotypes, for example between the primitive *Myotis* ($2n = 44$) and the highly derived *Lasiurus* ($2n = 28$) (Fig. 3).

The end point of karyotypic evolution in a higher category may take longer in one lineage than another. It is obvious, however, that the older the group, the more likely it is to have already achieved Stage III karyotypic stability and the younger the group the more likely it is to be chromosomally diverse.

In all three stages of the canalization process, some chromosomal alterations with no or little selective value may become established. A greater number of such "neutral" changes will become established in species with a high level of inbreeding and small deme size. However, it is our thesis that such "neutral" or "drift" events play a much less important role than do adaptive changes.

DISCUSSION

Unlike other models, the canalization model emphasizes the adaptive nature of the karyotype and implies that the karyotype is a major component of the "adaptive strategy" of an organism. This model is also based on the assumption that for each "adaptive zone" there is an optimum karyotype that can be evolved by rearrangements in the karyotype of the invader of that zone. Additionally, it should be recognized that most chromosomal evolution is phyletic in that a chromosomal mutation becomes characteristic of a lineage without the production of sister species (our model is not primarily concerned with the role of chromosomal change as an isolating mechanism in the speciation process).

Primary Reason for Chromosomal Diversity

Comparisons of models.—In previous models deme size and inbreeding, as a result of vagility, social structure, and other factors are given as the primary reasons why some species and genera are karyotypically stable, whereas others are highly variable. Previous models predict that taxa with large deme sizes have stable karyotypes with low levels of karyotypic evolution, whereas taxa with small deme sizes have greater variation and high levels of karyotypic evolution (White, 1978; Hall, 1973; Bush, 1975). In the canalization model the amount of chromosomal evolution is a function of the degree to which the optimum karyotype has been achieved for the adaptive zone occupied by the taxa. Assuming that the rate of chromosomal mutation is essentially a constant per individual, then the most important factor in any rearrangement surviving and becoming established is a function of the degree of fitness it confers to its possessor over individuals with the previous karyotype. If the karyotype for a species or a group of species is optimum, then the likelihood of any new karyotype becoming characteristic of the species is essentially zero (unless drift occurs). However, if the karyotype of a group of species is poorly adapted, then a higher percentage of the rearrangements will confer sufficient fitness to result in that karyotype becoming characteristic of the species. In the latter case, speciation will then generally be accompanied by the evolution of distinct karyotypes.

Some indirect data, which indicate that chromosomal types have selective advantages of sufficiently high value to result in the above process, are available (Berry and Baker, 1971; Patton, 1970; Staiger, 1954; Stebbins, 1950). We see no reason to believe chromosomal changes cannot be selected for by natural selection in the same way as any genetic change. Even if such mechanisms as preferential assortment and reduced chiasma frequency are not present, chromosomal changes will occur in populations if a change results in a level of fitness great enough to overcome the disadvantages of the heterozygosity bottleneck. Thus, a new adaptive gene arrangement could quickly become established in even a large Mendelian population.

Chromosomal variation of higher taxonomic levels.—Wilson and colleagues characterize frogs as having small amounts of chromosomal variation, but they possess a 22–44 range of diploid numbers (not counting polyploids). Other orders characterized by Wilson and his colleagues as having conservative rates of chromosomal evolution, such as bats, also possess considerable chromosomal diversity. For instance, in the family Phyllostomatidae (Baker, 1978; Gardner, 1977) the diploid number ranges from 14 to 46 and the fundamental number ranges from 20 to 68. Within some subfamilies, the range is also extensive (Phyllostomatinae, $2n = 26–46$; FN = 20–68; Glossophaginae, $2n = 16–32$; FN = 24–60; Carolliinae, $2n = 20–36$; FN = 36–62; Stenoderminae, $2n = 14–44$; FN = 20–56). If small deme size is a requisite for extensive chromosomal evolution, then to account for the extensive variation at higher taxonomic levels, the breeding structures of the ancestral populations of turtles and bats were radically different than those of modern species.

The canalization model predicts that the longer a taxon has occupied an adaptive zone, the more probable it will be that the taxon will have achieved karyotypic stability and the higher the taxonomic category at which chromosomal stability is found.

This general trend is quite apparent in the tables on rates of chromosome evolution in Bush et al. (1977, Table 1) and Wilson et al. (1975, Table 1). These authors have documented the average age of genera, rate of karyotypic changes, and rate of speciation (Bush et al., 1977, Table 2), for about 10 order level groups of mammals and several lower vertebrate groups. Among the mammals there is an inverse correlation between greater average generic age, and higher rate of chromosomal change and higher rate of speciation. Among the placental mammals, for example, horses, primates, lagomorphs, rodents, and artiodactyls have the highest rates of chromosomal evolution and speciation and are the youngest groups. The insectivores, carnivores, bats, and whales all have lower rates of chromosomal change and speciation and they are also all older than the above-mentioned groups. These data are compatible with the canalization model.

Frogs are a much more ancient group than mammals and have had more time for their karyotypes to become canalized than, say, rodents. The same can be said for turtles and even bats because they are also older than rodents. When turtles, bats, and frogs were younger groups, they underwent a similar period of intense chromosomal evolution now observed in rodents. Turtles are older and more chromosomally stable than bats, and bats are older and more chromosomally stable than rodents. This aspect of the canalization model is in direct contradiction to Wilson et al. (1975) who stated, "However, there is little or no dependence of karyotypic evolution on elapsed time." These authors derive an equation to relate time with chromosomal diversity. Although their data did not show a significant correlation, the average correlation coefficient and average slope were negative, which would be predicted by the canalization model.

Deme size and chromosomal races.—Small deme size, low vagility, and other factors are certainly associated with most well-documented examples of chromosomal races and with one exception, *Uroderma* (Baker et al., 1975; Greenbaum, 1978), these biological features characterize examples of possible speciation by chromosomal mechanisms. Factors that produce high levels of inbreeding (low vagility, social structure, isolated populations, and others) have a strong influence in allowing some types of chromosomal variation to survive. However, most chromosomal races in such taxa will prove ephemeral unless a variant is of sufficient selective advantage to ultimately become characteristic of the species or to allow invasion of a different niche. If the new chromosomal variant has such selective advantage, it will follow the prediction of the canalization model. If it is not highly adaptive, then it will not prove critical to the overall pattern observed in vertebrate evolution. If the karyotype is as adaptive as envisioned in the canalization model, then genetic drift, low deme size, and low vagility may result in prolonging the existence of less fit chromosomal variants by microgeographic isolation from populations possessing a more optimal karyotype.

Bush et al. (1977) and Wilson et al. (1975) hypothesize that the small deme size and rapid chromosomal evolution of mammals results in more rapid speciation. It is undoubtedly true that deme size affects speciation rates to some extent, and perhaps to some extent the number of species in an adaptive zone. However, what is more important is that ancient genera will seem to have lower rates of speciation simply because they are older. When a generic lineage first breaks into its adaptive zone it undergoes a period of relatively rapid speciation until it fills the zone. As time goes on, no increase in the number of species takes place because the zone is full, although there may be a replacement of ancestral species by descendant species that have attained a more "optimum" generic karyotype, characteristic of Stage III evolution. The older the lineage becomes the lower the apparent rate of speciation within that lineage because, to determine that rate, you divide the number of extant species by the age of the group. The point here is that if bats were studied at the same relative age that rodents are today, they probably would have had equivalent rates of chromosomal evolution and speciation.

Is the Nature of Evolution Different for Different Vertebrate Groups?

The canalization model suggests that there is no fundamental difference in the nature of evolution in diverse vertebrate groups. As to why there is more morphological diversity in mammals than in frogs (see *Significance of Chromosomal Variation*, above), Wilson and colleagues compared the amount of morphological diversity between two different taxonomic categories—Class Mammalia and Order Anura. A more appropriate comparison would be a mammalian order (such as Chiroptera or Rodentia) to the frogs or Class Mammalia to Class Amphibia. At this point it becomes evident that a comparison of morphological diversity between frogs and any large mammalian order is essentially of the same magnitude. As to why there is a difference between the ability of frogs and birds versus mammals in producing interspecific hybrids, we feel certain points need to be considered before concluding that altered regulator systems is an important reason that hybrids are not produced in mammals. It is true that mammals do not readily hybridize (relative to frogs and birds), but this is true not only of taxa that differ chromosomally (that might result in regulator gene problems), it is just as true of groups (such as *Myotis*) which have indistinguishable karyotypes (which should not have such developmental problems). The primary reason for the reduced hybridization in mammals is probably more sophisticated behavioral premating isolating mechanisms, not postmating chromosomal mechanisms.

We agree with Wilson and colleagues that structural gene changes occur at or near same rates within the groups and that chromosomal changes affect regulatory systems. But we do not agree that there are different types of evolution at work in these groups. The older groups, such as frogs, experienced their karyotypic revolution during Stage I which occurred long ago, when they first entered their adaptive zone.

How is the Canalization Process Redirected?

It is apparent that the process of karyotypic canalization has been redirected many times during the evolution of the vertebrates; otherwise, everything from fish to mammals would have identical karyotypes. Breaking into a new adaptive zone is what results in some new chromosomal mutations being adaptive, producing the revolution characteristic of Stage I or Stage II, depending on the width of the adaptive zone that is invaded.

Tests of Models

Canalization model.—In order for a model to be most useful, it should be stated in a manner subject to tests of Popperian falsification. Adequate tests of the canalization model primarily include correlating age with chromosomal diversity, and comparing chromosomal banding patterns among higher categories to determine inter- versus intra-higher category variation. Certainly, if it is found that there is not an inverse correlation between age and chromosomal diversity within many groups, this would represent a falsification of the model, and would mean that the canalization model is not of general applicability.

Deme size models.—A valid test of the deme size model would be variation in some nonmammalian old vertebrate group that has considerable variability in deme size. Turtles appear to us to be such a group. Marine turtles and species that inhabit large lakes and extensive river systems undoubtedly have large deme sizes and should show essentially no chromosomal diversity. Other species, such as softshelled turtles (*Trionyx*) and tortoises (Testudinidae) have low vagility, are frequently isolated in small subunits, and should reflect a level of chromosomal variability similar to that observed in mammals with equivalent deme sizes. We feel if the deme size model is to have any credibility it must be demonstrated in some of the vertebrate lineages older than mammals.

Another group that seems to be well suited as a test of the small deme size and canalization models is moles (Talpidae). If the deme size model is correct, highly fossorial, solitary mammals (as some moles are thought to be) would be expected to show a pattern of chromosomal variation similar to that of other fossorial mammals such as pocket gophers and *Spalax*. However, the Insectivora is an old group and the canalization model would predict that their karyotypes should be becoming canalized.

The Nature of Higher Categories

The canalization model suggests that higher categories undergo a series of stages in their development. Categories at or above the ordinal level represent such broad adaptive zones that chromosomal homologies cannot be deduced among higher groups, but below the ordinal level homologies can generally be identified. It also appears that there is a difference in the kind of chromosomal rearrangements that take place in Stage I (interfamilial comparisons) and Stage II (intrafamilial comparisons). Thus, the breaking into a ordinal level zone may be associated with a different genetic revolution than is involved in the breaking into a familial or lower level adaptive zone. An implication of the canalization model is that higher categories are real as suggested by Schaeffer (1976). The various categories are not merely "pigeonholes" that man has created, but in fact have evolutionary meaning.

In a communication such as this (as well as those presenting previous models), it is impossible to discuss all aspects of such an extensive process as chromosomal evolution; however, we do believe that there are more than adequate data (some of which are presented above) to justify the consideration of the canalization model as a viable alternative to previous models. It is in this spirit that we present our model.

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BIASES IN THE FOSSIL RECORD OF SPECIES AND GENERA

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INTRODUCTION

Many of the larger scale problems now being investigated by paleoecologists and evolutionary paleobiologists depend for their solution on having an accurate knowledge of the Phanerozoic history of taxonomic diversity. The problems are exemplified by the following questions. Has the number of species increased steadily since the mid-Paleozoic or was a steady state reached in at least some environmental realms or adaptive zones? Are temporal changes in the numbers of species and higher taxa basically unpredictable because of the complexity of causative factors or are there trends, cycles, or periods of equilibrium that are recognizable and amenable to rigorous analysis? Do geographic patterns of diversity (provincialism, endemism, and others) change in a predictable fashion in response to climatic or tectonic changes? Can the quantitative relationship between number of species and habitable area be applied on a world-wide scale to large evolutionary groups?

Most of these questions have been investigated to some extent in two important books—Valentine's (1973) *Evolutionary Paleoecology of the Marine Biosphere* and Boucot's (1975) *Evolution and Extinction Rate Controls*. In addition, many shorter contributions have explored a few of the questions in detail. For example, Flessa and Imbrie (1973) and Fischer and Arthur (1977) have analyzed diversity data for temporal patterns and cycles. The Fischer and Arthur work is particularly important because it concludes that diversity in pelagic biotas fluctuates with a rhythm of about 32 million years. Schopf (1974) and Simberloff (1974) have applied the species-area concept to Permo-Triassic changes in family diversity and to the question of mass extinction. Van Valen (1973*a*) applied a probabilistic model (the Red Queen Hypothesis) to the problem of extinction of higher taxa. Many other examples could be cited.

The main shortcoming of these and comparable works is that their basis in empirical data is limited. The published syntheses of distributions of fossil taxa in space and time are generally not adequate to provide truly definitive answers to the questions being asked. The problem is two-fold—first, tabulation of diversity data is an extremely time consuming job and is frought with procedural difficulties (sampling, nomenclatural problems, questionable records, and others) and second, raw data on fossil diversity are misleading because of the distorting effects of systematic biases. The best syntheses of data are those confined to single biologic groups that have been especially well monographed. The more comprehensive tabulations (Harland et al., 1969; Kukalova-Peck, 1973) are at too high a taxonomic level for many interpretive purposes. At the lower taxonomic levels (genus and species), theoretical work has had to rely on published tabulations of intelligent guesses (Easton, 1960; Van Valen, 1973*b*; and a few others). It is at the lower taxonomic levels where evolutionary and ecologic theory is most robust and it is at these levels where interpretive analysis may be most fruitful—given the proper data base.

The purpose of this paper is to evaluate our knowledge of Phanerozoic diversity at the specific and generic levels and to suggest ways of improving the quality of this knowledge. The emphasis will be on the fossil record of invertebrate animals.

SAMPLING CONSIDERATIONS

The fossil record is an exceedingly small sample of past life. The probability of any individual animal being preserved and later found is vanishingly small. It is only because so many individuals have lived in the geologic past that we have as large a fossil record as we do. Because fossilization is a rare event, a group of organisms having even a slight advantage in the preservation process will be vastly over-represented in the record. The fossil record is thus a strongly biased one.

Table 1.—*Numbers of taxa found in a sample from the Arnum formation (Miocene of Denmark) as reported by Sorgenfrei (1958) and rarefaction estimates of the numbers of taxa that would have been found had the sample been smaller. The estimates calculated from rarefaction have been rounded off to the nearest whole number.*

Taxonomic level	Actually found	Predicted for a sample of 500	Predicted for a sample of 100
Phylum	1	1	1
Class	3	3	2
Order	12	9	7
Family	44	24	14
Genus	64	31	17
Species	86	39	19
Specimen	2,954	(500)	(100)

Table 2.—*Estimates of preservability for a few biologic groups.*

Biologic group	Taxonomic level	Percent of living taxa with a fossil record
Brachiopods	family	100
	genus	77
Echinoids	family	89
	genus	41
Asterozoans	family	51
	genus	5
Bivalves	family	95
calcitic	genus	86
aragonitic	genus	54
freshwater	genus	27
Ostracodes	family	84
	genus	42
Arachnids	genus	2
	species	<1

Taxonomic Level

In general, the quality of the fossil sample increases as one moves up the taxonomic scale. This is because higher taxa (excluding monotypic taxa) inevitably contain more individual organisms than lower taxa. All things being equal, a taxon having the most individuals will have the highest probability of becoming part of the fossil record. Table 1 illustrates this relationship with a Miocene assemblage taken from a drill hole in Denmark (data from Sorgenfrei, 1958). The studied part of this assemblage was made up of molluscs and thus only one phylum (Mollusca) was reported. There were 2,954 specimens and any one of them would have sufficed to record the presence of the phylum. There were three classes in the sample (Gastropoda, Bivalvia, and Scaphopoda) but they were present in unequal numbers—only 47 of the 2,954 specimens were scaphopods. Thus, if the sample had been substantially smaller than 2,954, it is likely that the order Scaphopoda would not have appeared. By the same token, it is conceivable that a much larger sample would have yielded specimens of a fourth class. As one goes down through the taxonomic hierarchy, the likelihood of missing taxa increases in a systematic fashion.

The case just considered can be analyzed rigorously by rarefaction techniques (Sanders, 1968; Simberloff, 1972; Raup, 1975). It can be shown in the Danish Miocene case, for instance, that if 500 specimens had been collected, only 39 species and 24 families would have been found rather than the 86 and 44, respectively, that were found. Table 1 shows estimates for other taxonomic levels and other sample sizes.

An important corollary of the relationship just described is that as sample size increases, the ratios of lower to higher taxa increase systematically. In Table 1, there are 1.1 species per genus in the smallest sample and 1.3 species per genus in the largest sample. The number of families per order increases from 2.0 to 3.7, and so on. When sampling starts and only one specimen has been collected, all taxonomic ratios are inevitably 1.0. With increased sampling, the ratios approach their true values.

The most important element of sampling for taxonomic ratios is that the systematic increases just described mimic the temporal sequence usually postulated for an adaptive radiation in evolution.

Because paleontological sampling is nearly always incomplete, our knowledge of past life is much better at high taxonomic levels than at low. At the generic and specific levels, sample size is a factor that cannot be ignored and may actually be the dominant factor in influencing diversity data.

Variation in Preservability

It is a truism that some biologic groups in some habitats are more readily preserved than others. Extremes are easily recognized. Insects, for example, are vastly underrepresented as fossils relative to other groups because they lack hard skeletons and because their terrestrial habitats do not normally yield a good sedimentary record. At the other extreme, heavy shelled, infaunal, marine molluscs enjoy a much higher probability of preservation and thus make up a larger fraction of the record.

One way to quantify variation in preservability is to calculate the percentage of living taxa that have a fossil record. These percentages may be taken as a first approximation of differences in inherent preservability. Table 2 gives the values for a few fossil groups. This approach requires the tacit assumptions that all groups have had constant abundance throughout recent geologic periods and that all originated at the same time. These assumptions are patently false but the results are still valuable as a general guide.

The data in Table 2 show a wide range of values, yet for each group, preservability increases with taxonomic level. It is clear that fossil diversity data at low taxonomic levels should be corrected for preservability. From a statistical standpoint, one hundred fossil echinoid genera represent a considerably higher original diversity than one hundred fossil brachiopod genera. Comprehensive work on a correction system remains to be done, however.

Geographic Factors

The geographic distribution of fossil data is irregular and is influenced by many factors. That the geographic coverage is incomplete is immediately evident when one superimposes the distribution of fossiliferous rocks on a map of the world showing present-day biographic provinces. To cite an extreme case, the sedimentary record of the marine Lower Triassic is available in only a few regions. Africa, South America, and Antarctica are essentially devoid of record and the present oceanic areas are virtually closed to paleontological exploration for rocks of this age. With sampling as sparse as this, several large faunal provinces could easily be missed. The low taxonomic diversity for species and genera of the Lower Triassic may thus be an artifact of sampling.

Also, paleontologic exploration has not proceeded at equal rates in all areas because of variation in the distribution of practitioners. For example, of the fossil species described between 1900 and 1970, 24% were found in the United States. This is slightly more than were found in the combined areas of Central America, South America, Africa, and Asia (exclusive of USSR) (Raup, 1976*a*). Correction for this factor is nearly impossible because it is difficult to distinguish differences in sampling from real differences in diversity.

Idiosyncratic Variation in Sampling

In spite of the generally poor quality of the sample, the fossil record occasionally yields spectacularly good preservation. Such cases, commonly termed *Lagerstätten*, are scattered in an apparently idiosyncratic fashion throughout the Phanerozoic record. Classic examples include the Solnhofen limestone, the Mazon Creek shale, and the Burgess shale.

The influence of *Lagerstätten* on diversity data varies with taxonomic level. Because these assemblages contain organisms that are normally "unpreservable," they often provide the only occurrences of extinct taxa or the only fossil occurrences of extant taxa. The many "Middle Cambrian to Recent" ranges stemming from the Burgess shale play a significant part in diversity data at the order and class levels. But at the lower taxonomic levels (species and genus), the influence is minor because the total number of taxa involved is a small fraction of the total fossil record.

Cisne (1974) has proposed that the faunal lists for *Lagerstätten* can be used by themselves as a measure of standing diversity. He argued that by concentrating on situations where sampling bias is minimal, a more accurate picture of relative changes in diversity can be achieved. Cisne's suggestion is being implemented in a comprehensive manner at the specific level by Bambach (1975).

THE PULL OF THE RECENT

It has been suggested that the nature of the fossil record and the conventional methods of analyzing it carry built-in factors that make an increase in diversity toward the Recent almost inevitable (Cutbill and Funnel, 1967; Raup, 1972). This effect may be called the "Pull of the Recent." A spectacular example of this is shown in Table 3. Data on ranges of a large sample of Paleozoic genera and subgenera show that most taxa on this level are confined to a single geologic period, as indicated by the high values along the main diagonal in Table 3. For each period, the number of taxa extending into subsequent periods is small and decreases sharply as the range increases. If all the taxa originating in a period are considered as a cohort (the sum of the numbers in the first column constitutes the Cambrian

Table 3.—*Range data for genera and subgenera of invertebrates extracted from the* Treatise on Invertebrate Paleontology. *Table should be read as follows: 1,038 taxa originated and terminated in the Cambrian, 38 taxa originated in the Cambrian and terminated in the Ordovician, and so on.*

	First occurrences					
Last occurrences	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian
Cambrian	1,038	—	—	—	—	—
Ordovician	38	1,439	—	—	—	—
Silurian	7	180	512	—	—	—
Devonian	3	86	173	1,136	—	—
Carboniferous	3	19	20	104	774	—
Permian	3	20	24	59	243	470
Triassic	0	1	2	8	11	15
Jurassic	0	5	2	1	6	2
Cretaceous	0	4	0	6	5	5
Tertiary	0	3	0	1	3	1
Recent	30	25	13	25	24	16

Table 4.—*Effect of Recent records on inferred diversity in regular echinoids.*

	Number of genera using Recent taxa	Number of genera ignoring Recent taxa	Difference	Percent exaggeration
Pleistocene	47	15	32	213
Pliocene	51	37	14	38
Miocene	51	46	5	11
Oligocene	31	26	5	19
Eocene	54	50	2	4
Paleocene	25	23	2	9

cohort, for example), standard methods of population dynamics can be applied. Such analysis shows that the half-life of genera and subgenera is consistently about 25 million years. But the important feature of the data in Table 3 is the row of numbers at the bottom which records those taxa with fossil-to-Recent ranges. In the case of the Cambrian, the original cohort "decays" in a regular fashion through the Paleozoic—if allowance is made for minor sampling error as the number of survivors becomes small. If the 30 Cambrian-to-Recent ranges are ignored, the Cambrian data produce a reasonable survivorship curve. There is clearly something special about the 30 taxa that reportedly extend to the Recent. The same pattern can be seen throughout the table although the special nature of the fossil-to-Recent taxa becomes blurred as the diagonal converges with the bottom row.

What is special about the Recent taxa in Table 3? One possibility is that there are two fundamentally different kinds of genera—a large number that have a high probability of extinction early in their existence and a much smaller number that for some reason survive indefinitely. Such a discontinuity in survival potential is inconsistent with current evolutionary theory but cannot be ruled out absolutely. A much more likely explanation, however, is that the bottom row in the table is largely an artifact resulting from the Pull of the Recent.

The Pull of the Recent results from the following factors, arranged in descending order of importance:

(1) *Sampling Is More Complete in the Recent*

We know (from Table 2, for example) that many taxa are not preserved as fossils. Other taxa are quite readily preserved owing to a favorable combination of skeletal structure and habitat. Between these extremes, there is a continuum of intermediates such that some groups are found as fossils but have only a sparse and incomplete record. In these cases, the geologic range of the individual taxon is usually truncated by nonpreservation. It is unlikely, in fact, that the ends of the actual range will be recorded. But if the taxon is still living, the chances of this fact going undiscovered is remote particularly at generic and higher levels and among biologic groups important in the fossil record. Because sampling is so much better among living organisms, the geologic ranges of extant taxa are unlikely to be truncated at the Recent end. This may be the explanation for the 30 Cambrian-to-Recent taxa in Table 3—that is, point occurrences in the Cambrian combined with the existence of living species yields a long range. If these genera were not still living, most would probably remain as point occurrences or as genera with substantially shorter ranges.

Table 4 shows another example. As part of an earlier study of taxonomic diversity, accurate data on Cenozoic and Recent echinoid ranges were amassed (Raup, 1975). As is conventional, generic ranges were inferred from the stratigraphic distribution of species. For example, a genus having only Eocene and Miocene species was inferred to have existed in the Oligocene even though it was not found in Oligocene rocks. Similarly, a genus having only Eocene and Recent species was inferred to have existed throughout the Eocene to Recent span. The first column in Table 4 was developed by this method. The second column was constructed in the same way except that information from Recent records was not used. The effect of ignoring Recent records is indicated in the third and fourth columns.

Table 4 shows convincingly that for regular echinoids, at least, the Pull of the Recent produces an exaggeration in fossil diversity that varies from 4% (Eocene) to 213% (Pleistocene). There is a clear trend toward increasing exaggeration as the Recent is approached, as would be expected.

(2) *Misassignment of Fossils to Recent Taxa*

Although hard data are unavailable, it is likely that some fraction of the taxa with long fossil-to-Recent ranges are invalid in the sense that the grouping of species into the higher taxon is in error. This is presumably most common among organisms with simple morphology. Twenty-nine of the thirty Cambrian-to-Recent genera in Table 3 are radiolarians. Although taxonomic procedures vary greatly from group to group, most modern workers probably prefer to assign a fossil species to an extant genus rather than to erect a new genus in cases where morphologic evidence leaves room for doubt.

(3) *Recent Taxa Have More Fully Developed Taxonomy*

Because extant taxa almost always have more known species than extinct taxa and because the array of usable phenetic characters is generally greater, extant higher categories tend to be more finely subdivided than their fossil counterparts. Once this subdivision has been accomplished with living organisms, the subdivisions are more likely to be recognized in the fossil record. For example, the morphology of pedicellariae in living echinoids has proved valuable in the classification of species into higher taxa. Pedicillariae are rarely useful in the fossil record but, I submit, extraordinary efforts are made to recognize the same higher taxa as fossils. Although proof of this effect is elusive, it may have a significant influence in increasing apparent fossil diversity in those taxa that are still extant. And this has the statistical effect of artificially increasing apparent diversity as the Recent is approached.

Discussion

The three elements of the Pull of the Recent are difficult to disentangle. Nevertheless, summary data such as are presented in Table 3 can be used to assess the combined effect of the three elements. In Table 3, there are 133 taxa having Paleozoic-to-Recent ranges (the sum of the bottom row of the table from Cambrian through Permian). The 30 in the Cambrian and the 13 in the Silurian are the most likely to be artifacts of Recent records because they have zeros above them in the table. In the cases of the Ordovician, Devonian, Carboniferous, and Permian, the numbers in the bottom row are dominantly artifactual but may contain a few taxa with legitimately long ranges. Thus, something approaching 133 genera and subgenera are added to the diversity totals for all post-Paleozoic intervals even though they either did not exist or are in the data only because the sampling in the Recent is atypical. With each successive stratigraphic interval, the "load" of artifactual data increases. This effect is most significant in intervals where the generic standing crop is low for other reasons. For example, the standing crop of genera and subgenera for invertebrates in the Triassic, as inferred from ranges, is about 600. Even if only 100 of the 133 taxa referred to above are artifacts of Recent records, the Pull of the Recent is responsible for a 20% exaggeration of Triassic diversity (from 500 to 600)!

Although the quantitative evaluation of the Pull of the Recent is still at a primitive stage, we can look forward to a rigorous assessment when more data along the lines of Tables 3 and 4 have been amassed and analyzed.

EFFECTS OF AVAILABILITY OF FOSSILIFEROUS ROCKS

A bias deserving special attention stems from natural geologic variation in the quantity of sedimentary deposits through geologic time. It has been shown repeatedly that there is an irregular yet consistent increase in volume and map area of sediments through time (Gilluly, 1949, 1969; Higgs, 1949; Gregor, 1970; Blatt and Jones, 1975). That is, the volume and area of rock, *preserved and known*, per million years increases from Precambrian to Recent. The consensus interpretation of this phenomenon is that the increase is due simply to the fact that the younger rocks are least likely to have been eroded, metamorphosed, or covered.

Not surprisingly, the number of fossils (and therefore fossil taxa) is influenced by variation in amount of available rock. Gregory (1955) showed that there is a strong correlation ($r = 0.94$) between apparent generic diversity in vertebrates and the number of principal collecting localities. In fact, he concluded (pp. 598–599) that ". . . accidents of present-day exposure so strongly influence figures on the abundance and diversity of fossils that conclusions as to . . . times of organic diversification should be based upon other types of evidence." Simpson (1960) and Raup (1972) also argued for the biasing effect of variation in quantity of potentially fossiliferous rock although few hard data were available. A recent analysis, however, of about 70,000 species of fossil invertebrates shows that diversity is correlated with both geologic map area and estimated volume of sediments (Raup, 1976*b*). These correlations are statistically significant at the 1% level. Ironically, species diversity is more highly correlated with area and volume than area and volume are with each other. A multiple regression analysis of the same data by Sepkoski (1976) shows that although most of the variation in diversity is caused by sampling, differences in area of shallow seas also play a role. This effect is biologically real but can be seen only after the effects of rock volume and area have been removed.

As one moves up the taxonomic scale, the sampling effects described above decrease in influence. For genera, quantity of fossiliferous rock still has strong effects. Sampling is apparently of minimal importance at the family level and is virtually absent at the order and class levels. Except for classes with very few species or cases where preservability is low, the availability of fossiliferous rocks is adequate to insure a fossil record, which is reasonably free of bias stemming from sample size.

TOWARD BIAS-FREE ESTIMATES

Before accurate diversity curves for species and genera can be constructed, the new data must be filtered to remove the biases discussed in this paper. The two most important factors are the Pull of the Recent and the variation in quantity of fossiliferous rock. These two are important in part because they have the largest effect on diversity data and in part because their effects are time-dependent.

The Pull of the Recent has little if any effect on species diversity because species durations are very short relative to the geologic time scale. For genera, the effects are greatest in the late Mesozoic and Cenozoic. These time intervals contain many genera that are still extant and thus the better sampling in the Recent exerts a pull. The late Mesozoic and Cenozoic also carry a large accumulation of artifactual records of the Cambrian-to-Recent type discussed above in connection with Table 3. To remove these effects rigorously will require more data than are presently available. The data in Table 3 are preliminary and incomplete and Table 4 is based on only one class.

Filtering out the effects of area and volume of sediment is possible, but the results cannot be made bias-free with the data base available now or likely to be available in the near future. The basic problem may be exemplified by the Triassic. Species diversity for the Triassic shows a negative residual with respect to quantity of rock. That is, fewer species are recorded than would be predicted from rock quantity. The problem is that the deficiency could have resulted either from a true drop in number of species or from a surplus of unfossiliferous rock. In the case of the Triassic, the high frequency of terrestrial red beds makes the second alternative a possibility but a definitive answer is not possible at this time.

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TETRAPOD MONOPHYLY: A PHYLOGENETIC ANALYSIS

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INTRODUCTION

"What we really need is more fossils." This oft-repeated statement usually follows, both in print and in meetings, arguments concerning the relationships of primitive tetrapods. But we do have more fossils; in fact, we have more fossils than ever before and, because of new discoveries and newly prepared "old" specimens, we have over the past fifty years conspicuously enlarged the diversity of extinct forms as well as increased our knowledge of their structure. Yet Panchen (1975:290) writes ". . . the story of the early evolution of tetrapod vertebrae is certainly less simple and less certain than it appeared to be even less than ten years ago . . . ." Although his comment is directed toward one particular morphologic region, I think it characterizes feelings about tetrapod phylogeny in general. For example, Olson (1971:583) in a review of early tetrapod evolution stated ". . . the use of assumed phylogenies as bases for deductions concerning almost all of the problems of tetrapod origins have introduced such a mixture of objective and subjective analyses of data that dispassionate assessments are difficult and too infrequently encountered." Olson lays the blame on "assumed phylogenies" but I will argue here that the general lack of success in developing objective ideas about relationships is due to basic problems in methodology.

Tattersall and Eldredge (1977) analyze a similar situation in studies of hominid evolution. They suggest that ". . . phylogenetic hypotheses can be formulated at three different levels of complexity, each successively further removed from the basic data available" (p. 204). The first, and most objective, is the *cladogram,* a methodology advocated here and explained below. The second level, called *phylogenetic trees* by Nelson (manuscript) and Tattersall and Eldredge (1977) involves the recognition of ancestor-descendant sequences, even though this requires the addition of untestable assumptions and suppositions. The third and least objective type of hypothesis is the *scenario,* which is essentially a tree further encumbered by assumptions and speculations about selective forces, niches, key innovations, radiations, adaptive zones, and other notions that have become the hallmark of explanation couched in the jargon of the Synthetic Theory. The elements of a cladogram are usually implicit in a scenario and might be abstracted from it, but ". . . as things stand, the diverse components of scenarios are seldom separable, and much of the reasoning that goes into their construction is circular: the many elements involved feed back upon each other in an extremely intricate way" (Tattersall and Eldredge, 1977:205). "There is no methodology at all for the formulation of a scenario, with all its varied aspects of evolutionary relationship, time, adaptation, ecology, and so forth. In devising a scenario one is limited only by the bounds of one's imagination and by the credulity of one's audience . . ." (Tattersall and Eldredge, 1977:207).

My own examination of literature on the "fish-amphibian transition" suggests to me that nearly all hypotheses concerning this subject have been formulated at the scenario level with little or no effort to separate adaptive speculation from testable phylogenetic hypotheses. Representative examples of scenarios are Szarski (1962), Schaeffer (1965), and Thomson (1966*a*). This, rather than the use of "assumed phylogenies," is the source of the problem referred to by Olson above (1971:583). It is impossible to choose objectively among contradictory scenarios and the result of difficult and tedious work in exploration for and preparation of fossils is often simply the generation of new scenarios.

It is my feeling that the prominence of scenario creation has had a particularly subtle effect even on critical workers not easily swayed by *ad hoc* hypotheses. For example, Carroll (1969:427), whose work is clearly oriented towards phylogeny reconstruction per se rather than adaptive scenarios of the sort seen in Olson (1966, 1976), nonetheless describes the standard "parallelism scenario" even though he does not accept it: "From our knowledge of the reptilian-mammalian transition, we know that extensive parallel development of very similar structures and character complexes may occur independently in numerous lineages. It is conceivable that limnoscelids, solenodonsaurids and romeriids evolved independently from a group with the anatomy similar to that of *Gephyrostegus.* Similar selective pressure could produce the reptilian condition in each. In the absence of any evidence to the contrary, solenodonsaurids and limnoscelids may be included as reptiles since they have developed a typically reptilian palatal structure and atlas-axis complex."

This insistence on the *ad hoc* recognition of parallelism or convergence is unfortunate because it requires information that cannot be obtained in an objective system. It would be wonderful to have testable hypotheses of "selection pressure" and "adaptive zones" concerning Devonian tetrapods and to be able to relate these to morphologic parameters. Ideas of this sort must be relegated to the "scenario" level of explanation and should not be used as tests of phylogenies. In fact, the only way to argue for the presence of parallelism or convergence is the demonstration that two alternative phylogenies are still viable after testing. As Cracraft (1972:387) has said: "A judgement of convergence must be based on an *a priori* assumption of relationship. The fact that two taxa . . . might show a number of morphological differences cannot serve as an argument for nonrelationship. The latter can only be proposed once a relationship has been demonstrated between one of these taxa and a third taxon." An argument for parallelism or convergence is simply an argument (often unstated) in favor of one phylogeny over an alternative one.

Another aspect of scenario creation particularly evident in early tetrapod studies is the "derivationist" approach to character distributions. Because of the emphasis on ancestor recognition rather than the testing of monophyletic groups, much effort has been put into how the rhipidistian fin (or vertebral column, skull, or whatever) might be changed into a tetrapod foot. This sort of argument was probably of significance in the early days of evolution versus creation debates when series of recent forms or fossils were arranged with hypothetical intermediates in order to show how changes *might* take place between greatly divergent morphologies. However, this has become an argument for homology of structures, and, therefore, phylogenetic relationship.

I think a more empirical approach, clearly related to a philosophic framework of science within which ideas may be criticized and judged, will lead to greater progress in understanding the history of organisms. Such an approach begins with phylogeny reconstruction of the sort advocated here, but this is not to say that scenarios have no place in paleontology. We will always be interested in mechanisms and processes of change as well as the geometry of it, and even though I see little hope of developing testable hypotheses of this sort in the near future, it is truly impossible to test hypotheses that are not formulated at all.

My intention in this paper is to take two hypotheses that although commonly accepted often create considerable debate, and test them using shared derived characters. In this procedure I hope to point out problem areas and alternative views also worthy of test. I also hope that this treatment will serve as a basis for further studies of tetrapod relationships. It should not be construed that I think this study in any way "settles the question" of tetrapod monophyly nor necessarily provides a complete review of all the characters pertinent to this hypothesis. I have used all the characters that in my opinion are pertinent but this is based primarily on a study of the literature. I hope that new studies of specimens will suggest the use of new characters that can be used to test monophyly of the Tetrapoda.

METHODOLOGY

There are currently a number of competing methods of phylogeny reconstruction, and I have based my choice of method on a particular view of the philosophy of science. Some systematists argue that philosophic discussions are fruitless, a waste of time, and irrelevant; that the interesting and important job is to "do the work." There is a growing feeling among systematists, however, that objective choices can be made but that they are dependent on a basic philosophy of science that sets limits and objectives. A philosophy of science is like any other intellectual subject matter; a certain amount of thoughtful inquiry is essential to its acquisition.

Perhaps the most common view of science, held by both scientists and non-scientists alike, is the Baconian view, or induction. In this philosophy, science is supposed to be a fact gathering operation, which proceeds until a theory or generalization emerges from the accumulations and finally a proving or demonstrating experiment or observation proves the truth of the generalization. It may then take its place in the firmament of acquired knowledge and the seeker of truth moves on to the frontiers of the unknown to gather new data. This process is usually called induction and it has been criticized philosophically at least since Hume's day, and more recently scientists such as Einstein and Medawar (Magee, 1973) have argued that in reality induction does not describe the manner in which the acquisition of knowledge progresses. In phylogeny reconstruction, I am continually impressed by the falseness of the inductive method when workers state that there are not enough fossils to "prove" a phylogeny, or that phylogeny cannot be done because of an "incomplete" fossil record, both required elements of the inductive approach.

One of the primary difficulties with the inductive or Baconian philosophy of science is that it allows or even requires the recognition of truth. Most scientists are too skeptical to accept this, and even though they may use induction, they will argue that their conclusions are expressable only in terms of probability. One conclusion is said to be more probable than the next or with increasingly greater quantities of data, one's conclusions become more probable. But how can "more versus less" probable be dealt with objectively? How can one identify a "more probable" conclusion unless one knows the yardstick of comparison, that is, the "true" conclusion?

The problem, as has been pointed out by philosophers for some time, is that no matter how many observations have been made that are consistent with a generalization, another observation that is inconsistent with the generalization is always possible. In other words, no number of consistent observations can prove the truth of a generalization. An alternative view of science and the acquisition of knowledge is the hypothetico-deductive method, or, as Karl Popper, a noted exponent of this philosophy has characterized it, conjectures and refutations. This philosophy recognizes that although we may have found the truth in our hypotheses and generalizations, we cannot identify it. We can, however, identify hypotheses or ideas that are inconsistent with observations, and this is the focal point of Popper's view of science. Although we can never know when we have found the truth, we do know when we are wrong. In this philosophy, all ideas and explanations in science are advanced as unprovable hypotheses that are intended to be submitted to rigorous attempts at falsification. Falsification may be defined as the result of a test of a hypothesis in which one (or more) of the expectations (predictions) of the hypothesis is shown to be inconsistent with observations. Observation, in this sense, refers to a lower level hypothesis (that is, a more specific or less general hypothesis) that is not itself being questioned or analyzed at this time but that is susceptible to test. Those hypotheses that survive repeated attempts at falsification are the most useful for further work. Nothing, however, is permanently removed from criticism, nor accepted as true.

Karl Popper (1968*a*, 1968*b*; see also Magee, 1973, 1974) has been most responsible for a modern development of the hypothetico-deductive view of science, but the method of advancing ideas or conjectures and then attempting to test them by experiment and observation is an old one. The application of the hypothetico-deductive method to systematics is relatively recent, at least in a formalized explicit sense, although Ghiselin (1969) has argued that it was essentially the method used by Darwin. In any case, some recent systematic work has emphasized the use of the hypothetico-deductive philosophy (Bock, 1973; Bonde, 1974, 1975; Miles, 1973, 1975; Platnick and Gaffney, 1977; Wiley, 1975). Because Wiley (1976) has an excellent review of the method of phylogenetic reconstruction used here, only a short summary is given below.

Hypothesis

The simplest hypothesis of relationship is the statement—two taxa are more closely related to each other than either is to a third. An equivalent statement would be—two taxa have an ancestor in common that neither has in common with a third taxon. Much of the confusion about cladism can be dispelled by understanding this statement of the hypothesis. A three-taxon statement of this sort is best expressed in the form of a diagram, called a cladogram. Cladograms do not indicate the positions of ancestral taxa, even though they may be present, and each line does not necessarily imply the existence of a separate lineage (see Nelson, manuscript; Tattersall and Eldredge, 1977, for cladograms versus trees). A cladogram is meant to be a hypothesis of monophyly and an ancestor and its descendant is just as much a monophyletic group as two descendants from a common ancestor. The recognition of ancestors requires a further set of assumptions that I am not willing to make. In any case, despite the incongruence with tradition, ancestors are not particularly important in phylogeny reconstruction.

Each of the three taxa in the three-taxon hypothesis should be monophyletic. That is, they are not monophyletic by assumption but they should be susceptible to test for monophyly. However, it is not necessary that these tests for individual monophyly of the three taxa be completed before testing the three-taxon statement as a whole. When one of the taxa in a three-taxon statement is hypothesized as being non-monophyletic, it changes the hypothesis, making the original hypothesis logically irrelevant rather than false per se. In any case, it is clear that a hypothesis of relationships, such as the one advanced below for Tetrapoda, that does not include tests for monophyly of its constituent taxa, is less satisfactory than one that does.

Test

The use of cladistic techniques to test hypotheses of monophyly rests on the following basic hypothesis (or axiom, an assumption at this level of hypothesis formation but still subject to falsification; see Popper, 1968*a*, chapter III): strictly monophyletic groups (descendants of a single species) are often characterized by new features (that is, morphology, behavior, ecology, genotype, and others). Conceivably, new species may not have new features but if and when this occurs, I know of no objective criteria that will allow the recognition of new species. The word "new" in the basic hypothesis must be qualified. A new feature in my sense could very well be a character reversal and therefore not "new" in a temporal sense. However, it would still be new to the species in question. This simply means that character reversals are not disqualified, however inconvenient their appearance may be.

If we use the basic hypothesis stated above, we may test a hypothesized monophyletic group for a character[1] or characters in common not found in any other group. Hennig (1966) termed

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[1] Throughout this paper I refer to "characters" rather than "character states." As far as I can see all "character states" should be termed "characters" to avoid hypotheses of homology (higher level synapomorphy), which are not required and usually not tested.

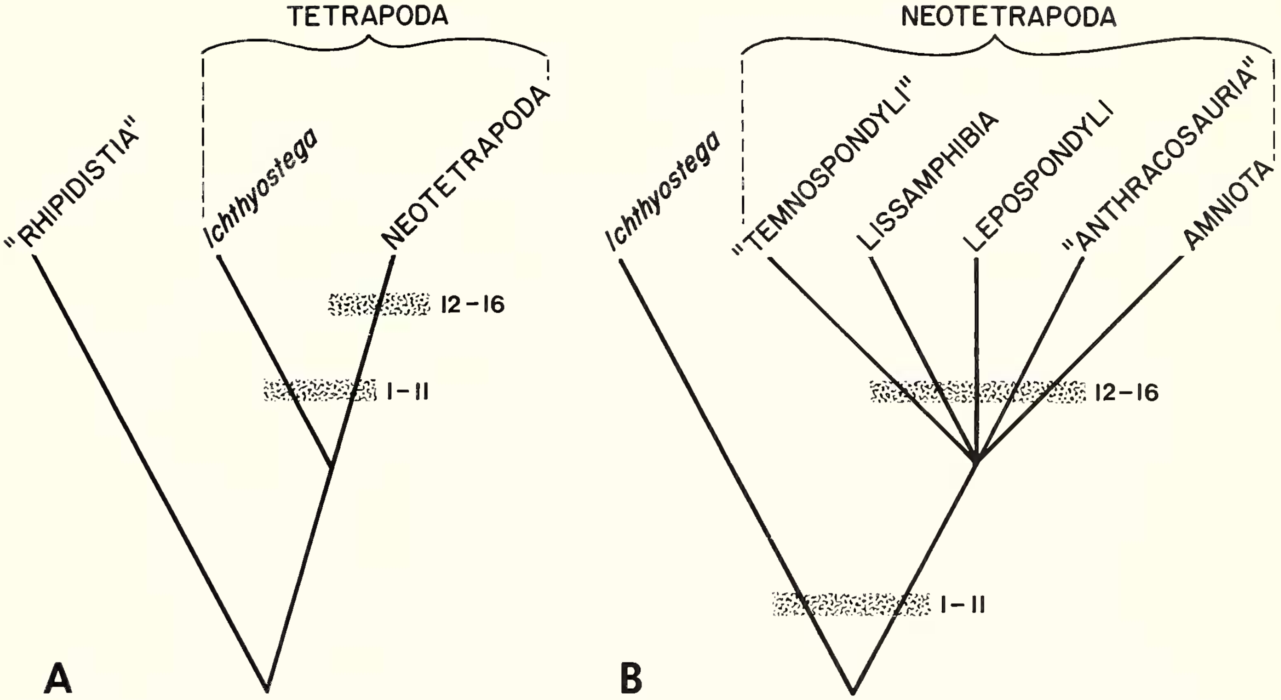

Fig. 1.—Cladograms of the two phylogenetic hypotheses discussed in the text. A) A three-taxon statement of monophyly of the Tetrapoda tested by characters 1–11. B) The statement that Neotetrapoda are monophyletic and consist of an unresolved multichotomy tested by characters 12–16. See text for discussion. Taxa in quotes are not hypothesized as monophyletic (see text under "basic taxa").

such unique or derived characters apomorphous and the common possession of such characters among taxa synapomorphy. In terms of the three-taxon statement, the test for monophyly of two of the three taxa is the presence of the same character in those two taxa but not in any other taxon. This is also called "out-group" comparison; it has been referred to frequently in the systematic literature and has been a prominent feature of systematics for a long time. In theory the out-group consists of all taxa outside the group being tested for monophyly but in practice one usually assumes the correctness of a higher level (more inclusive or more general) hypothesis of relationships and makes comparisons within it. If a character is consistently found within and only within a designated group then the test is consistent with (but does not prove) the hypothesis that the group is monophyletic. In and of itself this test does not mean very much but the important aspect of the test is that a character with the indicated distribution in a three-taxon statement falsifies two of the three alternative hypotheses relating the three taxa in question. This is the strength of the application of the hypothetico-deductive method of phylogeny reconstruction.

Wiley (1975, 1976) has, I think, demonstrated a fundamental relationship in his argument that the criteria used to test homology are the same used to test synapomorphy. For example, when we argue that the forelimb of a frog and the forelimb of a bat are homologous we are actually arguing that at some level (Tetrapoda) both taxa belong to a monophyletic group possessing a forelimb of a particular sort as a synapomorphy. Conversely, an argument proposing the use of forelimb morphology as a derived character testing the monophyletic nature of the tetrapods is also an argument that tetrapod forelimbs are homologous but only at some level of relationship; because as Wiley (1975, 1976) has emphasized, the words "homology" and "synapomorphy" as they are often used are not strictly equivalent. To continue this example, the forelimbs of two mammals would be homologous but not synapomorphous at the level of Mammalia. Homology and synapomorphy are both primarily tests for common ancestry and all of the classical criteria for homology determination, that is, development, topology, and morphology, the basic features of comparative biology, are all tests for monophyly.

The two hypotheses that I am presenting and testing here are diagrammed in Figs. 1 and 2. Fig. 1A shows the first hypothesis in terms of a three-taxon statement which would read as follows: *Ichthyostega* has an ancestor in common with (or is the sister group of) the Neotetrapoda. The non-monophyletic group "Rhipidistia" is indicated as the out-group, but the out-group for the tested characters may be considered as being all nontetrapod vertebrates; I have chosen rhipidistians for specific mention because they are generally the most similar to tetrapods and therefore are best suited for the search for characters presumed to be unique to tetrapods. In other words, if we find a character in rhipidistians (or any other nontetrapod) that is supposed to be a unique feature (derived character or synapomorphy) of tetrapods then this feature no longer can be argued to support the monophyly hypothesis. The first hypothesis (that is, that Tetrapoda is monophyletic) is tested by characters 1–11. The second

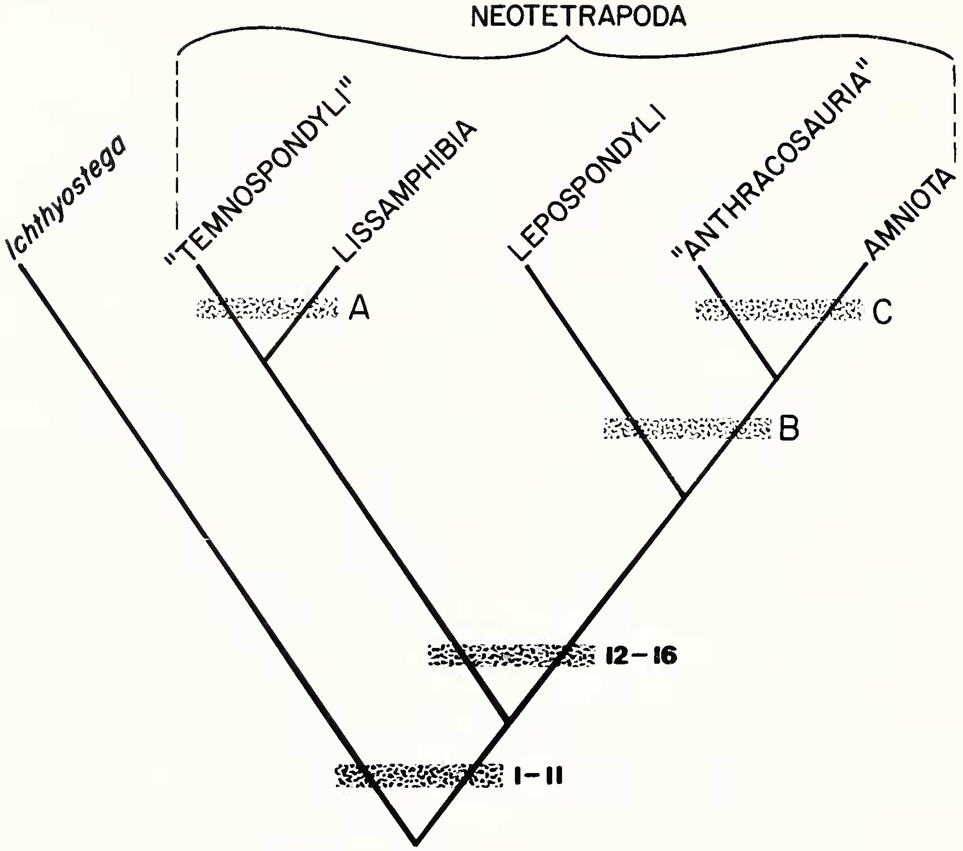

Fig. 2.—One of several possible hypotheses of relationship for the five suggested taxa in Neotetrapoda. This hypothesis is not dealt with in the text but is presented here to suggest future areas of inquiry. Tests would be developed by seeking characters with the distributions A, B, and C.

hypothesis is that the five listed taxa ("Temnospondyli," Lissamphibia, Lepospondyli, "Anthracosauria," and Amniota) constitute a monophyletic group Neotetrapoda. This group is not analyzed in terms of a three-taxon statement because I wish to specify as few hypotheses as possible below this level. Therefore, I use five taxa (termed "basic taxa," see below) in the form of an unresolved multichotomy (Fig. 1B). The outgroup for hypothesizing derived characters (12–16 in Fig. 1) for testing monophyly of Neotetrapoda is *Ichthyostega* plus rhipidistians and other fishes.

I show in Fig. 2 one possible three-taxon analysis of Neotetrapoda but I do not test this phylogeny with characters. In order to do so, derived characters should be sought and their distributions among the taxa determined.

BASIC TAXA

My hypothesis of tetrapod monophyly utilizes seven taxa, for some of which I am accepting hypotheses of monophyly, whereas for others I am not. The important point is that the units involved are all parts of subsidiary hypotheses of relationships that could be tested using shared derived characters. At this time it is not really necessary to examine these hypotheses even in the detail that I have. The few instances where my characters are absent (that is, limbless forms such as aistopods, apodans, snakes) are relatively well tested as tetrapods nonetheless. Rather, I am interested in suggesting areas for future inquiry and in showing what some hypotheses of lower tetrapod relationships look like when presented cladistically, and what some alternative hypotheses might be. I hardly consider this discussion any more than a series of suggestions and I want to emphasize that although I use these basic taxa hypotheses here, I do not consider any one of them to be particularly well tested at present.

"*Rhipidistia*"

The rhipidistians are here hypothesized as a nonmonophyletic group (hence the quotes) that consists of Choanata (sensu Miles, 1975) minus Tetrapoda (see below). This hypothesis requires that within the rhipidistians there is a monophyletic taxon that is the sister group of the tetrapods, but I am not hypothesizing what this group (or individual species) may be. *Eusthenopteron,* perhaps by virtue of being the best known rhipidistian, is often considered to be the most similar to tetrapods in that it has relatively well-ossified proximal limb elements that can be hypothesized as synapomorphous with tetrapods (Westoll, 1943*b*; Andrews and Westoll, 1970*a*, 1970*b*). However, some poorly known taxa have been reported that have more tetrapod-like features than *Eusthenopteron.* For example, *Elpistostege* (Westoll, 1938), *Hyneria* (Thomson, 1968*b*), and *Eusthenodon* (Jarvik, 1952) have tetrapod-like skull proportions, whereas *Sterropterygion* (Thomson, 1972) and *Sauripterus* (Andrews and Westoll, 1970*b*) have a tetrapod-like forelimb. Therefore I am making my comparisons throughout the Rhipidistia.

I am using here the hypothesis that rhipidistians plus tetrapods form a monophyletic group, the Choanata, as suggested by Miles (1975). The unique presence of internal nares (choanae) is the principal synapomorphy for this group. Dipnoans have a similar structure but this has been strongly disputed as a homologue of the choanae (see references in Panchen, 1967; especially those by Allis, Jarvik and Bertmar), and I am following this hypothesis. Although the coelacanths (Actinistia) have been widely accepted as near relatives of the rhipidistians (for example, Romer, 1966; Moy-Thomas and Miles, 1971; Miles, 1975) there is an alternative hypothesis that is currently gaining favor; this is, that the dipnoans are the sister group to the Choanata rather than the coelacanths (Løvtrup, 1977; Miles, personal communication). Either of these alternatives is satisfactory for my purposes because both require similarities between Recent dipnoans and Recent lissamphibians (that is, autostylic and monimostylic suspension, persistance of the chondrocranium) to be the result of convergence.

Alternatives:

1. Kesteven (1950, and references) presented 57 characters found in common between living dipnoans and living amphibians. He argued that crossopterygians (coelacanths and rhipidistians) lacked these features (to the extent they are determinable) and belonged to a group quite far removed from dipnoans and amphibians. Although to my knowledge a rigorous criticism of Kesteven's characters has not been published, my own examination of them suggests that few would survive a thorough analysis. The "soft" characters, however, could well be consistent with *Latimeria* being the sister group of dipnoans and tetrapods, if only the living groups are considered.
2. Jarvik (1975 and earlier) has argued for some time that urodeles plus porolepiforms are the monophyletic sister group of osteolepiforms plus remaining tetrapods (see Lissamphibia, below, for comments).

Ichthyostega

I am using the hypothesis that the described material of *Ichthyostega* is referable to one strictly monophyletic taxon, either a species or a group of species, that are characterized by the features noted by Jarvik (1952) for the genus *Ichthyostega,* and shown in his figures of the whole animals (Jarvik, 1955: Fig. 11), the skull (1952: Figs. 35, 36), tail (1952: Fig. 6), pelvis (1952: Fig. 5; 1964: Fig. 24), and hind foot (1952: Fig. 5; 1964: Figs. 25, 26). This hypothesis, however, can be criticized. Panchen (1975:634) has said: "Any conclusion about *Ichthyostega,* however, is weakened by the fact that the name may well represent a fauna rather than a taxon." Säve-Söderbergh (1932), when he described the first seven specimens, erected two new genera and five new species for their reception. Jarvik (1952) had a much greater number of specimens at his disposal but (as far as is determinable from the literature) none of the skulls are associated with the postcranial material and much of the postcranial material is disarticulated. In view of the probability that few of Säve-Söderbergh's types will allow the development of adequate diagnoses, it is easy to see why Jarvik's (1952) restorations were identified as *Ichthyostega* sp. Furthermore, Jarvik's description of *Acanthostega* (see below) added to the liklihood of more than one taxon being represented by postcranial material. Therefore, the hypothesis that we are dealing with one monophyletic taxon in "*Ichthyostega* sp." may very well be falsified in the future.

Romer (1947, 1966) and Jarvik (1952) have referred various forms to the Ichthyostegalia and Panchen (1973) has described a fragmentary specimen with opercular bones. I consider most of these taxa incertae sedis, but they are of sufficient interest to discuss here.

Jarvik (1952) described a new taxon, *Acanthostega*, based on three fragmentary specimens of temporal roofs. His taxon has the lateral lines in canals as in fishes and *Ichthyostega* and a reduced but present preopercular. The palate, snout, and postcranium are unknown. The otic notch is shallow as in *Ichthyostega* but *Acanthostega* is unique among amphibians in having a tabular embayment with a short tabular horn.

Crassigyrinus (Panchen, 1973) has a cheek with bone proportions more rhipidistian-like than occurs in *Ichthyostega*, but its lateral line system is in grooves not canals, a good neotetrapod (see below) character.

Both of these taxa are too incomplete to deal with reasonably in a phylogenetic analysis but they give an intriguing indication of the endless potential for novelties in the fossil record.

Westoll (1938) described *Elpistostege* as a primitive tetrapod, but Thomson (1969) says it is a fish. In any case, it has dermal bone proportions that are now known in both rhipidistians and tetrapods, so that it is no longer of particular interest phylogenetically. Romer (1966) assigned *Otocratia* and the colosteids to the Ichthyostegalia, primarily on the common absence of an intertemporal and the presence of a shallow otic notch, but Panchen (1975) has argued otherwise.

"*Temnospondyls*"

Temnospondyli is a term used by Romer in 1947 to include all labyrinthodonts (including ichthyostegids and stereospondyls) except anthracosaurs. I am using it in the later sense of Romer (1966) so that it excludes ichthyostegids but includes rhachitomes and stereospondyls. In this sense, it would be non-monophyletic under the hypothesis advocated here because it excludes lissamphibians (see below). Romer's (1947) diagnosis of temnospondyls is a list of characters that with few exceptions appear to be primitive for Tetrapoda. In fact, the only one of Romer's characters that might be derived is the four digit manus (Romer, 1947:79). The other characters are found in rhipidistians, *Ichthyostega*, and anthracosaurs. Furthermore, as I am using hypotheses suggested by Bolt (1969) and Estes (1965) that dissorophids are the sister group of Lissamphibia, the temnospondyls of Romer (1966) are paraphyletic unless Lissamphibia are included. The four digit manus would be consistent with a grouping of the temnospondyls and lissamphibians.

Loxommatids (Romer, 1947; Beaumont, 1977) are a good plesiomorphic sister group for remaining temnospondyls (including lissamphibians), which could be hypothesized as monophyletic using palatal vacuities and other features described by Romer (1947). The primitive condition of the vacuities would be the sort seen in *Edops* while the remaining temnospondyls and lissamphibians would possess the more advanced condition.

I know of no alternative hypotheses suggested in the literature, but the available character distributions (forefoot is unknown in loxommatids) would be consistent with loxommatids as the sister group of temnospondyls plus anthracosaurs.

Lissamphibia

I am here using this term in the sense of Parsons and Williams (1963), that is, that urodeles, anurans, and apodans form a strictly monophyletic group. Parsons and Williams' discovery of pedicellate teeth reawakened interest in living amphibians as a strictly monophyletic group. Jurgens (1971) has made a detailed study of the nose and concluded on the basis of specialized characters, that lissamphibians were monophyletic. However, little other work in this direction has been published. As Carroll and Currie (1975) have argued, the really weak point is the relationship of apodans. Apodans are so highly specialized in the loss of limbs and girdles, eye reduction, and skull morphology that few hypotheses about their relationships can be falsified at present. To me, an obvious procedure would be the assessment of primitive characters within apodans via a shared derived character analysis of their phylogeny. Comparison of this with primitive morphotypes of anurans and urodeles should be productive, as Jurgens has shown.

As with most of my other basic taxa, a non-monophyletic Lissamphibia might not affect tetrapod monophyly. If, for example, Carroll and Currie's (1975) hypothesis (see below) is accepted, apodan limblessness is nonetheless considered to be derived for that group and still consistent with tetrapod monophyly.

Among the alternatives to lissamphibian monophyly are the following ideas (restated to make them comparable) that have appeared in the literature.

1. Dipnoans and urodeles form a monophyletic group which is the sister group of rhipidistians and remaining tetrapods. Developed by Säve-Söderbergh (1934) and Holmgren (1933, 1949), criticized by Westoll (1943*a*, 1943*b*, 1943*c*), Schmalhausen (1968), and Thomson (1968*a*). Holmgren's hypothesis was based initially on similarities between the chondrocrania of dipnoans and urodeles and later on limb development.

2. Porolepiforms and urodeles form a monophyletic group that is the sister group of a monophyletic group containing osteolepiforms and remaining tetrapods. Jarvik has argued this hypothesis from 1942 until 1975 (the most recent reference I am aware of) and has changed from using snout and palate characters to many other areas. Nelson (1973) and Bonde (1975) correctly say that there has been no effort to explicitly analyze Jarvik's characters, pro or con, for synapomorphies, and that therefore the criticisms by Szarski (1962), Kulczycki (1960), and Thomson (1962, 1964, 1967*b*, 1968*a*) among others are not particularly telling to his argument. I think, however, that although most of these arguments do not serve as adequate tests of Jarvik's hypothesis, some of them, particularly Thomson (1967*b*, 1968*b*) do serve to dispute Jarvik's homologies and this would be critical to a synapomorphy analysis. And, as Nelson (1973:826) has said: "There is the possibility that his initial conclusions, based on conformity to type, were overextended enough to fatally bias his subsequent argument."

3. Lepospondyls, urodeles, and apodans form a monophyletic group which is the sister group of the remaining tetrapods. Romer (1945, 1947) advanced this hypothesis basing it primarily on patterns of vertebral development. Romer retreated from this position in 1966 following Parsons and Williams' (1963) work.

4. Apodans and microsaurs form a monophyletic group, sister group unspecified (Carroll and Currie, 1975).

5. Apodans are the sister group of the Amniota (Løvtrup, 1977).

6. Microsaurs are the sister group of urodeles plus apodans but excluding anurans (Gregory, 1965).

Lepospondyls

I use this group in their conventional sense (Baird, 1965), that is, consisting of aistopods, nectrideans, and microsaurs (including lysorophids, *Acherontiscus*, and *Trihecaton*). In view of the fact that the initial criterion for the group, holospondyly, is now known to be true only for aistopods and nectrideans (microsaurs have intercentra in a number of genera, Carroll and Currie, 1975; Carroll, 1968) it might seem that there are few characters uniting this group. Nonetheless, lepospondyl monophyly is the most viable hypothesis at present, and the lack of an otic notch, enlarged tabular, and strap-shaped concave occipital condyle might be suggested as shared derived characters.

Although many authors (see Panchen, 1977, and references) have argued that lepospondyls are not a natural group, there have been few arguments presented for alternatives. Thomson and Bossy (1970), however, argue for aistopod-nectridean-anthracosaur monophyly using the tabular-parietal contact. Microsaurs also have this feature and this is actually consistent with lepospondyl-anthracosaur-amniote monophyly (see Fig. 2). Bossy (1976) has used derived characters (accessory apophyses, intravertebral foramina, fused centrum) for a hypothesis of aistopod-nectridean monophyly.

Vaughn (1960, 1962) and others have suggested lepospondyl-amniote monophyly but it is not clear whether or not this would involve remaining lepospondyls as the sister group or not.

In any case, only Carroll's (1967) suggestion that lepospondyls evolved from holospondylous rhipidistians while rhachitomous tetrapods evolved from "rhachitomous" rhipidistians would be inconsistent with my argument of tetrapod monophyly. However, vertebral diversity among Choanata as presently known is great and there are few hypotheses that would be falsified by such distributions because as Panchen (1977, see also for most recent review of this subject) has remarked: ". . . the variety of vertebrae within 'rhipidistia' is so great that . . . almost any theory of the origin of tetrapod vertebrae could be corroborated by a well chosen rhipidistian" (p. 303).

"Anthracosaurs"

The anthracosaurs (here used in the sense of Romer, 1966, equals Batrachosauria of Panchen, 1972) are argued to be the nearest known relatives of amniotes in most traditional hypotheses (Carroll, 1969, and other references); that is, they would be the sister group of amniotes, using cladistic terms. Panchen (1972) argued that they are not near relatives of reptiles but are more closely related to temnospondyls. Panchen's (1975) diagnosis of Batrachosauria consists of characters that I would consider to be primitive for Neotetrapoda with these exceptions: tabular-parietal contact, vomers narrow between internal nares. Both of these characters occur widely in lepospondyls as well as in anthracosaurs and amniotes and could only be considered consistent with monophyly of these three together (as I have suggested in Fig. 2). Panchen (personal communication) has suggested that tooth structure (Panchen, 1970) and a small or absent post-temporal fossa may be synapomorphous for anthracosaurs.

Amniota

My hypothesis of amniote monophyly includes fossils and therefore utilizes preservable characters for tests. Carroll (1970:305) lists a series of nine characters that can be hypothesized as derived for this taxon. Some of them, such as the astragalus, absence of intertemporal, absence of palatal fangs, small or absent intercentra, and no otic notch, occur in microsaurs, but the pterygoid flange is a unique amniote feature. Furthermore, the detailed structure of the temporal region and the sporadic distribution of the astragalus in microsaurs (Carroll and Baird, 1968) suggest that these features are not homologous in both groups.

Monophyly of living amniotes has rarely been questioned but there have been statements of reptilian polyphyly concerning fossil groups (Olson, 1947; Vaughn, 1960).

SHARED DERIVED CHARACTERS TESTING THE MONOPHYLETIC NATURE OF TETRAPODA[2]

1. *Anterior (ethmosphenoid) and posterior (otico-occipital) moieties of braincase intimately united in adult with only a suture persistent (if at all), a distinct fissure as seen in rhipidistians absent, dermal skull roof region overlying braincase united without indication of transverse hinge seen in rhipidistians.*—In rhipidistian fishes and coelacanths the braincase is characteristically separated in the adult into an anterior ethmosphenoid moiety, and a posterior otico-occipital (Moy-Thomas and Miles, 1971) moiety. All tetrapods, with the exception of *Ichthyostega*, show no indication of this division in the adult and the solid braincase is here hypothesized as a derived condition for tetrapods. *Ichthyostega* is reported as having a suture separating the two moieties but it lacks the fissure seen in rhipidistians (Jarvik, 1954; Romer, 1937; Thomson, 1965).

In the dermal skull roof of rhipidistians the braincase articulation is reflected in a distinct transverse fissure between the intertemporal plus parietal and supratemporal plus postparietal. Apparently this fissure acted as part of the intracranial joint (Thomson, 1967*a*). In *Ichthyostega* and other tetrapods the bones on either side of this suture are close together rather than separated. Dipnoans and actinopterygians also have fused braincases but differ from tetrapods in the manner of fusion, elements incorporated, and relative proportions.

2. *Parachordal (otico-occipital) region of skull (area posterior to basipterygoid articulation) longitudinally compact in comparison to rhipidistians.*—The relative proportions of rhipidistian and tetrapod skulls have been one of the classic characters used in discussions of the "fish-amphibian transition." Romer (1937, 1941) first brought attention to this feature in his work on crossopterygians and some version of his figure (1941: Fig. 4) has appeared in almost every discussion of the "transition" (see especially Westoll, 1943*c*: Figs. 3 and 4; Schaeffer, 1965: Fig. 4; Schmalhausen, 1968: Fig. 49). More knowledge of rhipidistians, however, has shown that some rhipidistians (*Eusthenodon*, Jarvik, 1952; *Hyneria*, Thomson, 1968*b*) have parietal and postparietal proportions that are very similar to tetrapods. Furthermore, some tetrapods (*Greererpeton*, Romer, 1969) have very short preorbital lengths, as in rhipidistians. However, information on the braincase of rhipidistians and tetrapods seems to show that the relatively compact parachordal region is derived for tetrapods. Dipnoans lack a compact otico-occipital region and are similar to rhipidistians.

3. *Otic notch.*—*Ichthyostega*, temnospondyls, and anthracosaurs are characterized by an otic

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[2] With regard to my use of the terms Choanata, Tetrapoda, and Amniota as monophyletic groups in a system of relationships using rigorous tests, it is interesting to note Romer's comments in 1937 (p. 56): "Säve-Söderbergh . . . has proposed the term Choanata . . . to include these forms [Dipnoans, Crossopterygians] and their tetrapod descendants as part of a phylogenetic scheme of rather unusual character. The term is hardly necessary in any phylogenetic and taxonomic scheme for which there is adequate support, although it is highly useful in a more 'popular' sense, comparable to 'tetrapod,' 'amniote,' etc."

notch, a V-shaped cleft formed at the posterior margin of the skull between the tabular and squamosal. In *Ichthyostega* the notch is shallow in comparison to temnospondyls and anthracosaurs in which it is usually deeper and may have the supratemporal involved as well. *Ichthyostega* also has a preopercular bordering the otic notch, a presumed primitive tetrapod condition. Amniotes and lepospondyls have no otic notch and the primitive condition of the temporal region would be a relatively straight transverse edge. The structure of the transverse edge is different in lepospondyls and amniotes (see Carroll and Baird, 1968: Fig. 11, for what may be suggested as the primitive condition for each group) and a straightforward, most parsimonious hypothesis would be that the features of the temporal region in lepospondyls is synapomorphous for that group and the temporal region of captorhinomorphs is synapomorphous for amniotes, and that an otic notch is synapomorphous at the level of tetrapods and neotetrapods. This is the hypothesis I use here, but the literature is filled with papers that are concerned with various problems in the ear region, particularly with regard to amniotes (see Amer. Zool., 6(3), 1966, for a symposium on the ear region and references). However, I have not been able to find any that propose a serious falsification of the above hypothesis. Most are concerned with developing a derivationist hypothesis involving unknown intermediates (see Parrington, 1958; Panchen, 1975) so that a "labyrinthodont intermediate" (that is, the otic notch being primitive for all tetrapods) is not required in a search for reptilian ancestry.

4. *Single pair of nasals with or without a single median ossification (internasal).*—In rhipidistians multiple median ossifications occur anterior to the frontals and are bordered on either side by multiple pairs of bones. Tetrapods have only a single pair of nasals (sometimes lost or fused) with an internasal primitively, as in *Ichthyostega*.

5. *Stapes.*—It has long been hypothesized, primarily on embryological evidence, that the hyomandibular of fishes is homologous to the stapes in tetrapods (see Goodrich, 1930, and references). This hypothesis of homology is equivalent to the hypothesis that tetrapods and fishes with a hyomandibular form a monophyletic group. At the level of tetrapods unique features of the hyomandibular may be used to test monophyly of that group. The stapes of tetrapods may be characterized as having the following derived features in contrast to the hyomandibular of rhipidistians: a) expanded proximal footplate intimately associated with fenestra ovalis; b) no contact with an ossified operculum; c) distal portion small or unossified; d) overall small size in relation to skull.

The stapes is not described in *Ichthyostega* nor in anthracosaurs (Panchen, 1970) and the discovery of a stapes, particularly in *Ichthyostega,* that differed strongly in these features might seriously weaken the use of this feature. Stapes are reported, although sporadically, in temnospondyls and lepospondyls. Among Lissamphibia, salamanders lack a well-developed stapes and may lack one entirely. Even if the Lissamphibia are not monophyletic, a stapes may by hypothesized as a primitive feature for urodeles.

6. *Fenestra ovalis.*—The fenestra ovalis is a lateral opening of the cavum labyrinthicum and is usually occupied by the footplate of the stapes. Rhipidistians do not have a fenestra ovalis[3], whereas all tetrapods in which the area is known have a fenestra ovalis. The condition for the area is not described in *Ichthyostega,* however, and although I am hypothesizing this as a tetrapod synapomorphy, it may be a neotetrapod synapomorphy.

7. *Carpus, tarsus, and dactyly.*—The presence of fingers in the fore and hind limbs in company with definitive ankle and wrist joints are among the most distinctive tetrapod attributes. Andrews and Westoll (1970*a*) identify tetrapod features in the humerus, radius, and ulna of *Eusthenopteron,* but find no indication of tetrapod features in a more distal position. Holmgren (1949, and earlier) and Jarvik (1965) have disputed presumed homologies between the carpus and digits of urodeles versus other tetrapods by arguing that similarities exist between urodeles and non-tetrapods in the morphology of the carpus and digits. Schmalhausen (1968:252, 255, Fig. 154) and Thomson (1968*a*:294–301, Figs. 8, 9; see also Olson, 1971:594) have developed arguments against using the limb characters of Holmgren and Jarvik by disputing the supposed homologies between urodeles and non-tetrapods. I think these arguments are apt and consistent with my methodology[4] but more importantly both authors use the detailed morphology of temnospondyl and lissamphibian appendages to argue for a common ancestor possessing these features. The characters

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[3] Jarvik (1972:210) describes a fenestra ovalis in porolepiforms and osteolepiforms but as far as I can tell the proximalmost portion of the hyomandibular does not fit into any fenestra and the "fenestra ovalis" of Jarvik lies posterior to the hyomandibular.

[4] Even Bonde (1975:309) agrees, saying that Thomson "probably demolishes this very unconvincing argument for 'diphyly.'"

of both authors are not expressed in terms of primitive and derived but the structure of carpus and tarsus in urodeles, *Ichthyostega* (tarsus only), temnospondyls, and amniotes (see Thomson, 1968*a*), as presented by these authors is readily hypothesized as synamorphous for these taxa in comparison with fishes.

Although the primitive number of digits in tetrapods may be disputed, there is rarely any argument about homology of the five known digits. Even Holmgren and Jarvik (above) do not dispute the identification of digits I–V among the tetrapods used in their studies (including urodeles). This is based not only on the position of the digits but also upon their consistent relations to carpal and tarsal elements even when one or more digits are secondarily lost. The absence of fin rays also makes tetrapod limbs distinctive. The combination of all these features results in a series of synapomorphies testing monophyly for Tetrapoda.

The apparently universal presence of four digits in the manus of lissamphibians and temnospondyls may be a synapomorphy uniting these two groups or it may be primitive for all tetrapods. The manus of *Ichthyostega* is not known but the close agreement of the carpus in temnospondyls and anthracosaurs suggests that five fingers in the manus is the primitive tetrapod condition. Also the common, but not universal occurrence of four digits in the manus of lepospondyls weakens the possible use of this as a temnospondyl-lissamphibian synapomorphy.

Howell (1935) and Schaeffer (1941) argue that there is no evidence for more than five digits in the manus and pes and that the prepollex and postminimus do not represent lost digits (Schaeffer, 1941, suggests that calling them pre- and postcarpale would be more accurate).

8. *Pectoral skeleton free from skull; post-temporal, supracleithrum, and anocleithrum absent; scapulocoracoid relatively larger than dermal shoulder girdle elements.*—Andrews and Westoll (1970*a*:219, and following) give a good comparison of this region between *Eusthenopteron* and tetrapods. As in other areas, detailed information on *Ichthyostega* would allow greater precision in comparisons of this sort. These features are universally present in tetrapods (except in the case of the scapulocoracoid, which is absent in some forms, that is, aistopods, apodans, snakes).

9. *Iliac blade of pelvis extends dorsally to level of vertebral column and is attached to vertebral column by an ossified sacral rib (or ribs).*—In *Eusthenopteron* there is no evidence of ossified sacral ribs although Andrews and Westoll (1970*a*) feel that a cartilaginous rib was present. At least one sacral rib and a well-developed iliac blade is present in all tetrapods, again with the exception of limbless forms.

10. *Well-developed ischiac ramus of pelvis, well-developed pubic symphysis (along with a generally large ventral portion of the pelvis).*—No rhipidistian approaches tetrapods in the development of these pelvic features, and these features are universal among tetrapods with the exception of limbless forms.

11. *Ossified ribs well developed and directed ventrally.*—Ribs are absent in nearly all rhipidistians but are present in *Ichthyostega* and nearly all other tetrapods. *Eusthenopteron* is the only rhipidistian definitely known to have ribs but they are small and dorsally directed. Well-developed and ventrally directed ribs are widespread in actinopterygians but this distribution would be plesiomorphic for this character only if the Choanata were not monophyletic and if the actinopterygians were the sister group of the tetrapods. Ribs also occur in two coelacanths (*Chinlea* and *Diplurus*) but this appears to be autapomorphic for those taxa.

SHARED DERIVED CHARACTERS TESTING THE MONOPHYLETIC NATURE OF THE NEOTETRAPODA

The Neotetrapoda[5] is the group of tetrapods which are the sister group of *Ichthyostega*, that is, temnospondyls, anthracosaurs, lepospondyls, lissamphibians, and amniotes, as characterized here. The five characters listed below are found universally throughout this group and no discussion of character contradictions is needed. They are listed in numerical sequence following the Tetrapoda characters for ease of reference (see Figs. 1, 2).

12. *Persistent notochord excluded from braincase in adult, parachordal (otico-occipital) region formed without significant contribution from notochord.*

13. *Preopercular and opercular (subopercular) ossification absent.*

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[5] "Eutetrapoda" might be more appropriate but it has been widely used by Säve-Söderbergh (1934) for a group of tetrapods excluding urodeles and to adopt this might cause confusion.

14. *Median bony fin supports with lepidotrichia absent.*

15. *Lateral line system absent or in grooves, enclosed in bony canals.*

16. *Ethmosphenoid and parachordal (otico-occipital) portions of braincase solidly fused in adult, not separated by suture.*

SUMMARY

The theory of relationships that the Tetrapoda are a strictly monophyletic group (in the sense of Hennig) is tested using the following derived (synapomorphous) characters:

1. Anterior (ethmosphenoid) and posterior (otico-occipital) moieties of braincase intimately united in adult with only a suture persistent (if at all), a distinct fissure as seen in rhipidistians absent, dermal skull roof region overlying braincase united without indication of transverse hinge seen in rhipidistians.
2. Parachordal (otico-occipital) region of skull (area posterior to basipterygoid articulation) longitudinally compact in comparison to rhipidistians.
3. Otic notch.
4. Single pair of nasals with or without a single median ossification (internasal).
5. Stapes.
6. Fenestra ovalis.
7. Carpus, tarsus, and dactyly.
8. Pectoral skeleton free from skull; post-temporal, supracleithrum, and anocleithrum absent; scapulocoracoid relatively larger than dermal shoulder girdle elements.
9. Iliac blade of pelvis extends dorsally to level of vertebral column and is attached to vertebral column by an ossified sacral rib (or ribs).
10. Well-developed ischiac ramus of pelvis, well-developed pubic symphysis (along with a generally large ventral portion of the pelvis).
11. Ribs well developed and directed ventrally.

A second theory of relationships suggests that the Tetrapoda consists of two sister groups, the Devonian tetrapod *Ichthyostega* and the Neotetrapoda. The Neotetrapoda is a term coined here to refer to the group consisting of the Temnospondyli, Lissamphibia, Anthracosauria, Amniota, and Lepospondyli. The following shared derived characters test monophyly of the Neotetrapoda:

12. Persistent notochord excluded from braincase in adult, parachordal (otico-occipital) region formed without significant contribution from notochord.
13. Preopercular and opercular (subopercular) ossifications absent.
14. Median bony fin supports with lepidotrichia absent.
15. Lateral line system absent or in grooves, not enclosed in bony canals.
16. Ethmosphenoid and parachordal (otico-occipital) portions of braincase solidly fused in adult, not separated by suture.

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